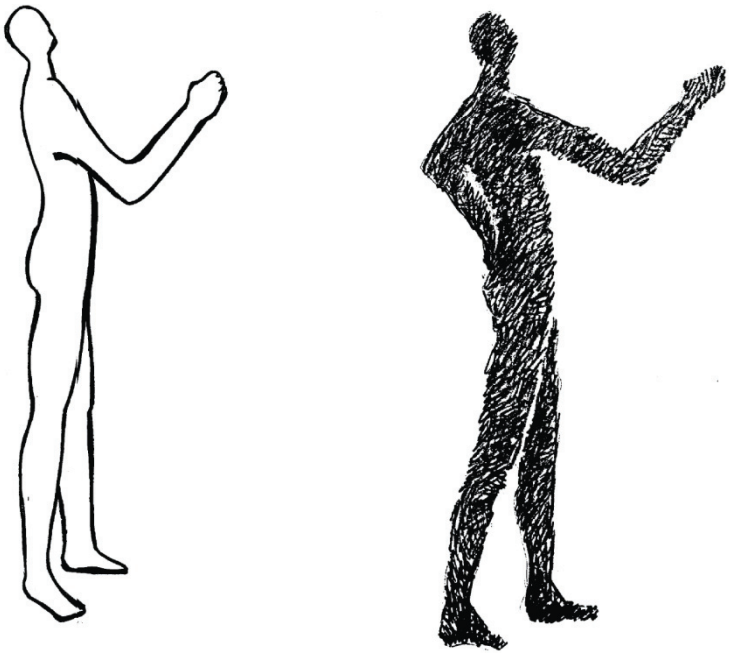
Managing Redundancy at Multiple Levels of Motor Control

Jurjen Bosga



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Managing Redundancy at Multiple Levels of Motor Control

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Prologue

Here we formulate some basic questions that we have addressed in our study of managing redundancy in motor control. Where relevant we will also specify the assumptions that we adopted in our approach.

A well-developed science is able to address two basic questions about the object it studies. First *how* does a phenomenon occur and second *why* does it occur? Trying to answer the second question requires scientists to apply the rigid frame of linear causality, i.e. everything that happens has a cause from the past. Typically, in dealing with the past and the present the theory of reflexes (Sherrington, 1906) is based on such form of causality. Circular causality, on the other hand, does not presume that phenomena necessarily occur because of a linear cause-effect sequence (cf. Kelso, 1995). Instead it emphasizes that the intrinsic dynamics of phenomena themselves may cause and maintain their evolution. Even though at several places in the present thesis we apply the methodology from dynamical-systems theory to the study of redundancy management in motor control, we have adopted a linear causality scheme when formulating our research questions and goals.

One of the salient features of phenomena pertaining to animate nature is their purposefulness, i.e. their relation to a certain goal, a feature inapplicable to phenomena of the inanimate nature (Feigenberg, 1998). Thus, phenomena of animate nature raise a third question. What is their *purpose*? Most movements made by humans are indeed directed towards achieving future states, the definitions of which are formed within their brains, a process that Tommaso d'Aquino (1225 - 1274) described with his theory of intentionality. In this context, Nicolai Bernstein wrote, "Goal, understood as encoded in the brain as a model of the desired future, defines processes that should be considered as goal-oriented …. The whole dynamics of the purposeful struggle with the help of appropriate mechanisms form a complex which should be united under the term activity" (Bernstein, 1990).

Critical questions concerning the exact nature of the relationship between perception and goal-directed movements were already formulated in ancient Greece some 2,500 years ago amongst the followers of Plato and Aristotle. Platonic doctrine embraced perception as a passive phenomenon stating that the world is represented internally as a collection of imperfect copies of ideally presented forms. In contrast, Aristotelians upheld the basic assumption that perception is active, i.e. the observer acts in a world to acquire the forms of objects to comprehend the nature of the forms by logic and induction. Accordingly, the actively moving heart was the seat of comprehension instead of the motionless brain, which served merely to cool the hot blood. In spite of their irreconcilable claims, both views share the notion that representations are crucial to the study of thought. In contemporary cognitive

neuroscience, representation is used as a counterfactual presentation reflecting the structure of the information that does not necessarily carry information about the entity it represents (Grush, 1997). It is, in very rough terms, a model of the target that is used off-line to try out possible actions, so that their likely consequences can be assessed without having to actually try those actions or suffer those consequences (Craik, 1943). It is this cognitive definition of internal representations that we adhere to in our study of redundancy management in motor control. We presume that in goal-directed task performance humans create expectations about the consequences of their actions and these expectations function as hypotheses that can be tested internally without directly taking action in the world.

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Chapter 1

Introduction

This chapter describes the motivation for our study of redundancy management in human motor control and introduces the main research question that we have addressed. Furthermore, the organization of the dissertation is outlined, and the topics addressed in the subsequent chapters are briefly introduced.

The Motivation

Today, the gold standard in clinical trial design is the double-blind randomized placebo-controlled study with two arms (Kaptchuk, 1998; Kaptchuk, 2001). One arm of the trial consists of a group of randomized patients who are given the active treatment, whereas the second arm consists of a group that is given the placebo — an inert treatment that mimics the active one in *all* respects (Colloca & Benedetti, 2005). The response to treatment brought about by the *belief* that one is receiving treatment is the placebo effect. The effect is explained by a positive change in mood and behavior occurring when one person touches another and shows care for them, pays attention, stirs hopefulness and provides encouragement (see Brown, 1998; Talbot, 2002). Because 'placebo exercise' is merely pointless there is no adequate way of conducting placebo-controlled studies with respect to physiotherapeutic exercise interventions. Furthermore, relationships between impairments, functions and disabilities are weak or nonexistent (e.g. Duncan, Goldstein, Matchar, Divine, & Feussner, 1992). Despite these facts, patient groups remain positive about physiotherapy and argue for greater access (Keus et al., 2004). Therefore, on the face of it, physiotherapy is the ultimate placebo (Stack, 2006).

However, one gratefully exploited feature of the motor system by physiotherapy in treating impairments of the movement system is redundancy (see also Shumway-Cook, & Woollacott, 2007). We have excess resources in many parts of our body, and this property allows us to perform the same task in many different possible ways. Redundancy improves reliability and flexibility in the motor system and potentially provides patient groups with unsurpassed adaptability in performing daily life activities. Thus, the need to understand the fundamental nature of the human movement system both normally and in pathology is perhaps one of the most important goals for research to ultimately impact physiotherapeutic practice (Winstein, Wing, & Whitall, 2003).

This dissertation reports a series of experiments on the management of redundancy at multiple levels of motor performance and as will be highlighted in the epilogue

can provide clinicians with an alternative source of evidence to help weigh their options during clinical reasoning.

Redundancy

One of the key challenges of cognitive neuroscience is to understand the principles that govern redundancy control, i.e., how the adaptive human system, at all its hierarchical levels, extracts from a large set of available control dimensions the minimum number of dimensions that is needed to act adequately.

Seemingly effortless we reconstruct the environment from the incoming stream of, often ambiguous (unclear), sensory information to generate unambiguous goal-directed behavior. On the perception side, we perceive the external environment by using multiple sources of sensory information derived from several different modalities, including vision, touch and audition. All these different sources of information are efficiently merged to form a coherent and robust percept. Depending on the type of information, different combination and integration strategies are used and prior knowledge is often required for interpreting the redundant sensory signals to come up with a solution given the ill-posed problem, or one-to-many mapping, of perception (Ernst & Bülthoff, 2004). On the execution side, we interact with the environment by selecting appropriate body configurations (postures) and control the complex biophysical properties of our body with a highly distributed circuit in the central nervous system (CNS) to move and satisfy the intent of our action i.e., to achieve our aims. However, the motor system is composed of an overwhelming number of accessories and an infinite number of combinations of these parts can be used to produce a particular body configuration to reach the stated goal.

For example, the musculoskeletal system is made up of large number of joints and muscles that provide many degrees of freedom, both with respect to the kinematics and the dynamics of movements. When defined in extrinsic spatial dimensions along which a joint can rotate, generally referred to as the three axes of a Euclidean X, Y and Z coordinate frame, the number of rotational degrees of freedom at different joints can range from one to three. In addition, the number of musc1es acting across a joint exceeds the number of rotational degrees of freedom in that joint whilst each muscle has a large number of motor units with various properties. Translations of the multi-articulated skeleton system from muscle activity are influenced by a variety of muscle and limb mechanics. Finally, the hierarchically organized CNS is made up of a spinal cord that includes motor neurons and interneurons, the brainstem including regions such as the reticular formation and vestibular nuclei, the subcortical structures like the basal ganglia gating the top-down information stream from cortex to spine, whilst the highest level is provided by the cerebral cortex, which supports a large and adaptable motor repertoire. These numbers explode when

we consider the degrees of freedom that come into play when we perform a motor task together with other human beings.

Such redundancy, or abundance of possible solutions to achieve the same goal, is beneficial to the sensorimotor system as it makes the search for a solution more likely to succeed. For the researcher, however, redundancy becomes a problem when we try to understand the mechanisms underlying the management of the degrees of freedom (DOF) of the motor system.

This dissertation aims at forwarding research in the field of motor control to uncover underlying motor-control strategies that enable redundancy management across multiple levels of motor control.

Redundancy, parallelism and degeneracy all play a major role in the impressive flexibility, reliability and robustness of biological systems. In general, redundancy refers to the quality or state of being redundant, that is: excessive; or supernumerary. In preparing a manuscript for publication, redundancy can have a negative implication: superfluous, repetitive or duplicate. However, in the study of language, redundancy is considered a vital feature for the purposes of error detection in communication. It shields a message from possible flaws in transmission (unclarity, ambiguity, noise). In this way, it increases the odds of predictability of a message's meaning. Whilst parallelism relates to the architecture of biological systems, which frequently includes many pathways that execute similar or related tasks, degeneracy is defined in a structural view as the ability of elements that are structurally different to perform the same function. Because structurally different elements may produce different outputs in different contexts, degeneracy should be distinguished from redundancy, which occurs when the same function is performed by identical elements (Tononi et al., 1999). We therefore define redundancy in this dissertation in a functional manner, i.e. as the ability to perform the same task in more than one possible way (see Latash and Turvey, 1996; Zatsiorsky et al., 1998).

Nicholai Bernstein (Bernstein, 1996) was one of the first to recognize a need for integrating knowledge on evolutionary biology, musculoskeletal form and function, biomechanics and observations of goal driven behavior to explain motor behavior. He emphasized the notion of a control hierarchy spanning multiple levels of the motor system, based on increasing complexity from muscle to spine to brain, with a supraordinate level for action formation at the top of this hierarchy. He had developed his theory of multi-level hierarchical control of voluntary movement around “the degrees of freedom problem”. In performing a new and unfamiliar motor task, Bernstein (1967) postulated that the novice is required to (re)organize the control of an overwhelming number of degrees of freedom in successive stages. First, a portion of the degrees-of-freedom set is initially eliminated thereby allowing the novice to reach the goal albeit with course behavior characteristics during task performance. Next, the degrees-of-freedom are gradually reintroduced

into the motor system and incorporated into larger coordinative structures. In the final stage, this organization becomes more economical, in the sense that biophysical forces (reactive, frictional and inertial) are exploited to the fullest, enhancing efficient, flexible, reliable and robust motor performance. Since then a number of different approaches exist in the literature that have emphasized part(s) of Bernstein's analyses or posed alternative mechanisms of redundancy management. We turn to these developments next.

Elimination

One approach is that the CNS reduces the number of DOF to the ones necessary to perform the task.

An initial solution to skill acquisition is to "freeze out" a portion of the degrees-of-freedom set. This can be done for individual degrees of freedom by keeping the joint angles or the whole body "rigidly, spastically fixed", thus allowing no or very little movement in the joints (Newell, 1991; Vereijken et al., 1992a). Improvement in skill would be characterized by a gradual release of the rigid control of the degrees of freedom and their incorporation into a dynamic, controllable system.

A related position comes from the observation that in some circumstances, movement takes place within a sub-space of the full space of mechanically possible movements. Evidence for such constraints comes from Donders' and Listing's law which, when applied to eye movements, states that the angular gaze positions do not routinely make use of all three DOFs but are constrained to a two-dimensional surface when the head is stationary (Donders, 1875). Donders' and Listing's laws might describe fundamental constraints which are imposed on the planning of arm postures. They could be implemented for a single arm joint or for multiple joints constrained by the CNS to act as a unit (Marotta et al. 2003). However, when the orientation of the hand is externally constrained by an object's geometry the upper arm (as compared to the forearm) complies more with Donders' and Listing's laws (Liebermann, Biess, Friedman, Gielen & Flash; 2006).

Coordination

In biological systems, coordination is defined as the spatiotemporal organization of elements i.e., things are (re)arranged in space and time.

In motor control, coordination can be described macroscopically, in terms of the ordering of body and limb motions relative to environmental objects and events or in terms of body configurations with respect to task requirements, or they can be described more microscopically, for example, the strength of correlations between neurons and how these correlations are related to the stimulus that is driving a particular motion.

A traditional intuition is that the human movement system is hierarchical, with each level solving a particular class of motor problems in the coordination or assembling of an act (Bernstein, 1996; Jackson, 1898; Weiss, 1941). In Bernstein's functional hierarchy, the level responsible for forming synergies of large muscle groups and different patterns of locomotion is referred to as the level of muscular-articular links or synergies. From this functional point of view, terms such as coordinative structure (e.g., Fitch, Tuller, & Turvey, 1982), uncontrolled manifold (Latash, Scholz, & Schöner, 2002), and coordination mode (Balasubramaniam & Turvey, 2004) have been nominated. Synergy conveys the notion of a collection of relatively independent degrees of freedom that behave as a single functional unit. This means that the internal degrees of freedom take care of themselves, adjusting to their mutual fluctuations and to the fluctuations of the external force field, and do so in a way that preserves the functional integrity of the collection (Turvey, 2007).

Within this context, the temporary coupling of actuators into motor synergies by moving two or more joint complexes in close phase relations has been put forward as a strategy in which the central nervous system might solve redundancy (Cole & Abbs, 1986; Santello, Flanders & Soechting, 1998; D'Avella, Saltiel & Bizzi, 2003; Ivanenko, Grasso, Zago, Molinari, Scivoletto, Castellano, Macellari & Lacquaniti, 2003).

Another aspect is that many so-called "degrees of freedom" are anatomically coupled i.e., forces exerted by biarticular musc1es can result in rotations in joints that they span. This means that the specific action of biarticular musc1es in multijoint movements might give rise to a specific activation pattern for monoarticular and biarticular musc1es (Van Ingen Schenau, 1989).

Optimization

Evolution, development, learning and adaptation, each on a different time scale improving our behavioral performance, provide a justification for quantifying task goals as cost functions and applying the sophisticated tools of optimal control theory to deduce detailed behavioral predictions (reviewed in Todorov, 2004 and in Seif-Naraghi & Winters, 1990).

Impetus was given to this notion by Flash and Hogan (1985) who were impressed by the regularity of hand-path kinematics in simple point-to-point positioning tasks and suggested that such movements are performed as if the mean squared rate of change of acceleration is minimized (Rosenbaum, 1991). Other minimization models have been proposed as well. For single-actuator movements it has been proposed that the central nervous system uses motion plans that are defined in terms of joint angles (Uno, Kawato & Suzuki, 1989; Nakano, Imamizu, Osu, Uno, Gomi, Yoshioka & Kawato, 1999; Rosenbaum Loukopoulos, Meulenbroek, Vaughan & Engelbrecht, 1995; Rosenbaum, Meulenbroek, Vaughan & Jansen, 2001). Combined with,

respectively, the minimum torque-change and minimum jerk principles the neuromotor system is supposed to solve the redundancy problem quasi-automatically.

Regardless of the nature of the reference systems in which the preparation of hand displacements takes place at various levels of the neuromotor system, experiments have shown that movements are always planned in such a way that the execution of these plans is robust against the variability that is inherent to the motor system (Harris, 1998; Harris & Wolpert, 1998).

Exploitation

A number of studies have used biophysical modeling techniques to investigate the mechanisms that physically cause motion (see Zernicke & Schneider, 1993).

In general, these studies examine the influences of active and passive inverse joint torques dynamics. Active joint torques and forces are those that are generated primarily by muscle action, whereas passive joint torques and forces include gravitational force, frictional forces, torques within the joint and inertial forces and interactive torques i.e. torques transferred from other body segments. For example, Thelen (1998) used the inverse dynamics approach to examine the influences of active and passive inverse joint torques dynamics and forces on the reaching and grasping of young infants during their first year of life. They found that infants recruited passive joint torques and forces more effectively with skill acquisition, implying that their dependence on active torques and forces decreased.

In a same vein, Schneider and Zernicke (1989) used the inverse dynamics approach in a task requiring rapid arm movement. They observed that participants were able to increase hand velocities and accelerations, produce smoother hand trajectories and realize lower movement time as a result of efficiently complimenting and counteracting passive torques by active torques and forces. Both these studies support Bernstein's (1967) influential view that adaptive motor behavior entails exploitation of, rather than resistance to, physics (e.g., Newell and Vaillancourt, 2001).

Allocation

Different tasks can be defined by different constraints, or the order of the same constraints may vary depending, for example, on whether grace, speed, or accuracy is most important. This approach also implies that motor performance is not per se optimal or efficient and is worth considering in the view of ideas promoted by two prominent thinkers in cognitive science.

One is Herbert Simon, who won the Nobel Prize in Economics for showing that optimization does not apply to all human decision-making (Simon, 1955). Rather

than optimize, Simon showed, decision-makers *satisfice* – a term Simon coined to refer to finding satisfactory if not optimal solutions. Simon later turned these ideas to the analysis of human cognition (Simon, 1989).

The other important thinker is Amos Tversky. One of Tversky's important contributions was the notion of *elimination by aspects* (Tversky, 1972). This term refers to the winnowing of possible solutions based on their failure to satisfy ever more specific requirements. Deciding whom to hire to fill a faculty position illustrates this approach. Typically, a department looks for someone in some area of study (the most important requirement), who has a strong record of research (the second most important requirement), who teaches well (perhaps the third most requirement), and who will be a team player (perhaps the fourth important requirement). The person who is hired is someone who escapes cuts at the most levels. He or she may not be optimal. The department and the candidate simply try to do the best they can.

Rosenbaum, Meulenbroek, Vaughan, and Jansen (2001) proposed that elimination by aspects is used in motor planning. The starting point for their proposal was Bernstein's (1967) challenge to explain how particular movement patterns emerge when physical tasks can be achieved in infinitely many ways. The solution proposed by Rosenbaum et al (2001) was that actors define tasks in terms of prioritized requirement lists or *constraint hierarchies*. According to Rosenbaum et al. (2001), the selection of a particular motor solution for a task is achieved as described above: All possible solutions that do not meet the most important constraint are eliminated, then all possible solutions that do not meet the second most important constraint are eliminated, and so on. The theory developed by Rosenbaum et al. (2001) made it possible to account for a large number of phenomena concerning motor learning and motor performance and proved useful in simulations of multi-joint prehension (Meulenbroek et al., 2001; Rosenbaum et al., 2001; Vaughan et al., 1996) and handwriting (Meulenbroek et al., 1996).

Delegation

One way redundancy is managed is that plans for behavioral sequences are structured hierarchically. Accordingly, the highest-level representation of a sequence to be produced corresponds to the sequence's main constituents, lower-level representations correspond to lower-level constituents, and so on (Mackay, 1982).

For example, kinematic analysis of the arm movements in a drawing and handwriting task showed that the shoulder and elbow movements are tightly coupled and generate the whole movement but corrections needed to fulfill the task requirements are generated at the more relatively loosely coupled distal joints (Lacquaniti, Ferrigno, Pedotti, Soechting & Terzuolo, 1987; see also Soechting, Lacquaniti & Terzuolo, 1986; Lacquaniti, Soechting & Terzuolo, 1986).

Furthermore, in the Leading Joint Hypothesis (LJH), Dounskaia (2005) has provided evidence that in multi-articular limb pointing movements and reaching there is one (leading) joint that creates a dynamic foundation for motion of the entire limb whilst corrections needed to fulfill the task requirements are generated at the subordinate joints. The leading joint motion generates powerful interaction torques at the other (subordinate) joints. The role of the subordinate control structures is to regulate the interaction torques and to create the net torque that results in the motion of the end-effector required by the task.

An alternative theoretical basis for addressing the degrees of freedom problem is the notion of stability (Schöner 1995), i.e. the capacity of the system to return to a given state after a (phasic) perturbation has driven the system away from that state. From a control-theoretical point of view, stability is a requirement to reliably achieve a motor goal and motor plans are therefore made in terms of stable degrees of freedom. According to the Uncontrolled Manifold Hypothesis (UCM hypothesis; see Latash, Scholz, & Schöner, 2002), the CNS differentiates the primary relatively stable variables for the nervous system's control of an act in task space from the secondary relatively unstable variables.

Outline of Dissertation

The next five chapters of this dissertation are written as standalone reports and comprise our research on the virtue of redundancy. The last chapter contains a discussion and conclusion of this thesis and some suggestions for future research.

From Chapter 2 though Chapter 6 we focus on five levels of redundancy management viz., intrapersonal multijoint level, intrapersonal movement-parameter level, intra- and interpersonal force level, interpersonal movement-parameter level and interpersonal multijoint level. In Chapter 6 we tested the generality of the Leading Joint Hypothesis to serve as an overarching control structure for multi-level management of redundancy.

In the remainder of this introductory chapter we will summarize the research questions and methods that we adopted in the series of studies reported in this thesis. The reader will inevitably note some overlap in the Method sections in Chapter 5 and Chapter 6 because both chapters focus on two different research questions within the same experiment. The discussion of the results of the experiments and the formulation of their implications can be found in Chapter 7.

Chapter 2

This chapter addresses the effect of articular conformity of the shoulder joint on the stability of inter-joint coordination in circular drawing movements and appears in

Bosga, J., Meulenbroek, R.G.J., & Swinnen, S.P. (2003). *Human Movement Science, 22(3),* 297-320.

In this study, we investigate the stability of intrapersonal coordination of shoulder, elbow and wrist joints and evaluate the extent to which articular conformity of the shoulder joint co-determines the stability of inter-joint coordination in circular drawing movements. Participants performed clockwise and counter-clockwise circular drawing movements at nine locations in the mid-sagittal plane. The task was acoustically paced at 1.0, 1.5 and 2.0 Hz and performed without visual control. Because the six degrees of freedom arm system is overspecified to perform the two functional degrees of freedom task, we determine phase relationships between the shoulder/elbow and elbow/wrist joint rotations to reveal the stability of the coordination dynamics that exist at the intrapersonal multijoint description level.

It has been shown that the coupling of joints in the arm is partially effected by the stabilizing role of poly-articular muscles, by inertia (Bolhuis, Gielen & Van Ingen Schenau, 1998), by movement frequency (Kelso, Buchanan & Wallace, 1991) and that the proximal shoulder/elbow joint pair is coupled relatively stronger than the distal elbow/wrist joint pair. However, the glenohumeral joint rotates around axes that are instantaneous and is dependent on the configurations the arm adopts. This 'built-in mechanical play' (cf. Kapandji, 1974) potentially provides the glenohumeral joint with more (or less) mechanical degrees of freedom than its primary axes of rotation would seem to suggest.

We therefore expect that certain arm configurations will most likely be influenced by intra-articular translations that occur in the shoulder as a result of rotating the shoulder in areas with a low articular conformity. We expect that these positions are associated with a decrease in stability of shoulder-elbow coordination, as reflected by an increase in the standard deviation of the variability of the continuous relative phase.

Chapter 3

In Chapter 3 we describe the means by which people vary movement parameters to satisfy more than one constraint at a time in a repetitive motor task and the chapter appears in Bosga, J., Meulenbroek, R.G.J., & Rosenbaum, D.A. (2005). *Journal of Motor Behavior, 37(6),* 437-46.

In this study we use a novel approach of inferring deliberate control from kinematics in tasks that are mainly motoric. Our *paradigm* is based on observations that large-amplitude arm movements tend to be performed at low frequencies by means of shoulder and elbow rotations, whereas small-amplitude arm movements tend to be performed at higher frequencies by means of wrist and finger rotations (Rosenbaum, Slotta, Vaughan, & Plamondon, 1991). Asking participants to depart from these

movement patterns (e.g., to produce fast shoulder movements or slow wrist rotations), requires them to refrain from relying on intrinsic amplitude-frequency relationships and instead to activate less natural, possibly more attention-demanding, control regimes (cf. Zelaznik, Spencer & Ivry, 2002; Swinnen & Wenderoth, 2004).

We investigate these biophysical inter-dependencies between movement amplitude and frequency (Kay, Kelso, Saltzman & Schoner, 1987; Rosenbaum et al., 1991) by studying the continuous drawing of ellipses (see also Meulenbroek, Thomassen, Van Lieshout & Swinnen; 1998). The presented loop pattern is displayed on the writing surface by means of the LCD video and approximates a normal cursive writing trace combined with a constant rightward progression. The loop pattern's height (3, 6, 9, 12, or 15 mm) and corresponding widths (3.5, 7.0, 10.5, 14.0, or 17.5 mm) are to performed with movement frequencies of either 1, 2, 3, 4, or 5 Hz.

Participants are supposed to match the amplitudes and frequencies of their movements to target values that vary from trial to trial. Typically, goal directed behavior is co-determined by the errors that people produce and the subsequent corrections of these errors (Elliott, Hansen, Mendoza & Tremblay, 2004). By scrutinizing the amplitude and frequency errors and subsequently determining the incidence and size of parameter-error changes as well as the success of such changes, we seek to identify those movement-parameter adjustments that are primarily due to deliberate attempts by the participant to meet the task goal.

We predict that a large number of parameter changes will result from exploiting (or following) natural biomechanical tendencies. However, we also expect an appreciable number of parameter changes will be deliberate because they defy the biomechanically given inverse relation between amplitude and frequency to prioritize their movement goals.

Chapter 4

This chapter investigates redundancy control in a virtual lifting task performed by two subject-pairs (dyads) and appears in Bosga, J., & Meulenbroek, R.G.J. (2007). *Motor Control*, *11(3),* 235-58.

Because lifting an object together requires the cooperation of two people it is an attractive task to study interpersonal coordination in joint performance. First, it allows us to determine the extent to which joint-action coordination is reactive or proactive. In addition, it allows us to investigate how groups deal with redundancy. How multiple degrees of freedom are contained in joint-action situations has hardly been studied before and we reason that a controlled study of a virtual joint-lifting task can fill this gap. Our virtual lifting task is performed by subjects individually (solos) or in pairs (dyads) who are asked to generate isometric forces. The task consists of generating an upward pressure with the left and right index finger on load cell

transducers (lifting phase) after which these forces need to be stabilized and maintained for a two-second period (holding phase).

When the task is performed with four hands, dyads are confronted with a redundant situation and between-hand force coordinative structures (synergies) at the interpersonal level can, in principle, be formed. In addition, because dyads only receive relative slow online visual feedback of their partners' actions, the output to the lifting task is composed of both actors' actions thereby masking the individual contribution to the task. This means that actions carried out by one partner are not directly observable for the other.

We therefore expect actors to adapt to the dynamics of their joint contribution as expressed by increasing stable interactions of balancing the bar and we therefore take systematic covariations between the redundant (supernumerary) force-producing hands in redundant joint-action conditions to reflect between-subject synergies that are brought about by adaptive processes in sharing the task.

Chapter 5

One of the central questions that we address in this chapter is whether we can differentiate between incidental and deliberate control of Rocking-board movements by the dyads. This chapter appears in Bosga, J., Meulenbroek, & R.G.J., Cuijpers, R. (2007). Interpersonal Movement Coordination in Jointly Moving a Rocking Board. In N. Gantchev and G.N. Gantchev (Eds.), Proceedings of Motor Control Conference MCC2007, (pp. 36-43). Sophia: Academic Publishing House.

In this study we verify whether our *paradigm* (see Chapter 3) can also be applied a task in which subject pairs coordinate their movements when deliberately trying, on a Rocking Board, to track a visually presented motion pattern. In particular, we ask our subject pairs to jointly produce side-to-side rocking movements on the Rocking Board in nine conditions covering three amplitudes (8, 18 and 28 degrees) and three frequencies (0.4, 0.6 and 0.8 Hz).

We contrast two conditions that we expect will modulate the extent to which dyads can exert deliberate control over their task performance. In one condition the subjects face each other and they thus are continuously given both haptic and visual feedback of their and their co-actor's movement consequences. In the other condition, the two subjects perform the task back-to-back thus preventing them from seeing each other. In the latter condition, the consequences of the co-actor's performance can only be picked up haptically. Given the key role which the visual modality is supposed to play in interpersonal movement coordination (Schmidt & O'Brien, 1997; Richardson et al., 2006), the frequency of intentional motion parameter changes is expected to be lower in the back-to-back than in the vis-à-vis condition.

Chapter 6

In Chapter 6 we address intra- and interpersonal coordination of dyads when performing cyclical motion patterns on a Rocking Board and the chapter has been submitted as Bosga, J., Meulenbroek, R.G.J., & Cuijpers, R. Intra- and Interpersonal Movement Coordination in Jointly Moving a Rocking Board (submitted). *Experimental Brain Research.*

In this study, we extend the study described in Chapter 5 to test the generality of Dounskaia's (2005) Leading Joint Hypothesis (LJH) to serve as an overarching control structure for hierarchical management of redundancy at the intrapersonal and interpersonal level. Because the study in Chapter 4 has shown that relative slow on-line visual feedback accounts for less proficient performance by dyads, as compared to individual performance, we now conduct a kinematic analysis of the joint-coordination patterns that two *mechanically* linked dyads display while moving a Rocking Board along prescribed amplitude and imposed frequency combinations. To execute the side-to-side rocking task on the Rocking Board, participants are confronted with an ill-posed problem, i.e. they are forced to reduce their many mechanical degrees-of-freedom into a one degree-of-freedom rocking movement.

By deriving body-segment angular excursions and analyzing the continuous relative phase and time-lagged cross-correlations between relevant joint excursions at the intrapersonal and interpersonal level, we can determine whether the coordination dynamics at the intrapersonal and interpersonal level are controlled by the same principal.

Chapter 7

Chapter 7 contains a discussion and conclusion of this thesis and some suggestions for future research.

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Chapter 2

Stability of Inter-joint Coordination during Circle Drawing: Effects of Shoulder-joint Articular Properties

Abstract

The present study addressed the effect of articular conformity of the shoulder joint on the stability of inter-joint coordination during circular drawing movements. Twelve right-handed participants performed clockwise and counter-clockwise circular drawing movements at nine locations in the mid-sagittal plane. The task was paced acoustically at 1.0, 1.5 and 2.0 Hz and performed without visual control. Displacements of seven infrared light emitting diodes that were fixated at relevant joints were sampled at 100 Hz by means of a 3D-motion tracking system (Optotrak 3020). From these data, shoulder, elbow and wrist angular excursions were derived as well as the continuous relative phase of the proximal and distal joint pairs of the arm. The results confirmed earlier observations that the shoulder and elbow are more strongly coupled than the elbow and wrist in sagittal-plane movements. However, a typical characteristic of the architecture of the shoulder joint, that is, its built-in mechanical 'joint play', was shown to induce a position-dependent variation in inter-joint coordination stability. We conclude that besides polyarticular-muscle induced synergies and inertial coupling, articular conformity of the shoulder joint constitutes an additional determinant of inter-joint coordination stability that, to date, has been neglected.

Introduction

In this study we investigate the stability of the coordination of shoulder, elbow and wrist rotations during circular drawing movements performed in the mid-sagittal plane. The aim of the study was to evaluate the extent to which articular conformity of the shoulder joint co-determines inter-joint coordination stability in cyclical motor tasks. To date, various temporal and spatial variables have been identified as control variables that modulate the stability of relative phase (as indexed by its variability), not only in single-limb multi-joint movements but also in inter-limb, multi-limb and two-person coordination. In previous studies, coordination stability has been shown to vary as a function of movement frequency (Buchanan, Kelso, & Fuchs, 1996; Fink, Foo, Jirsa, & Kelso, 2000; Kelso, 1984), inertial loading (Jeka & Kelso, 1995), movement direction (Swinnen et al., 1998), arc curvature (Buchanan, Kelso, & de Guzman, 1997), vision (Buchanan & Horak, 1999) and posture (Buchanan & Kelso, 1993). The effects of articular conformity on coordination stability, however, have been neglected. Based on specific joint-surface characteristics that will be explained in the following, we expected that the strong coupling between shoulder and elbow rotations would break down when the circular drawing task was performed at certain locations in the mid-sagittal plane.

Articular conformity

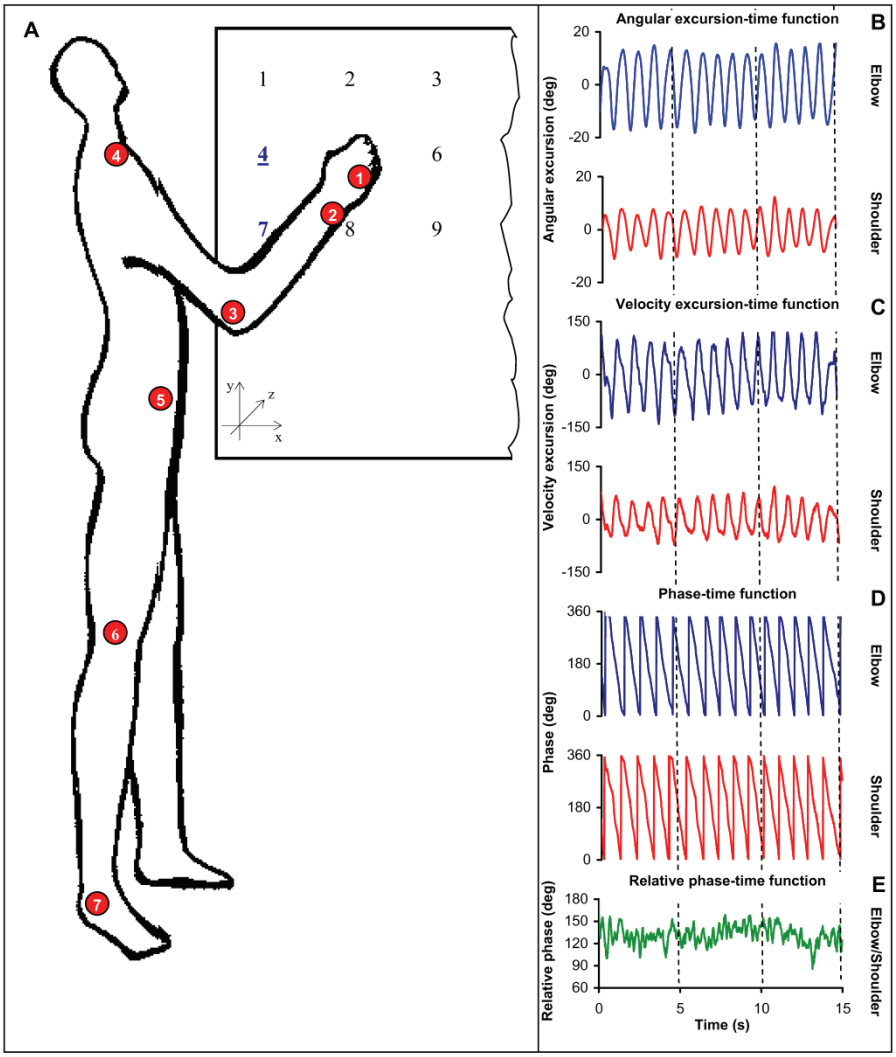
Joints are unions of two or more bones and have two main functions: to permit motion and to provide stability (Wilk, Arrigo, & Andrews, 1997). Whereas high male joint mating surface curvature is related to joint mobility, high female joint mating surface curvature is related to joint stability under loads of different orientation (Hamrick, 1996). The geometry of joint rotations is quite complex. The axes around which a joint can rotate are evolutive, that is, their positions and orientations change during movement. Consequently, we should always refer to them as instantaneous rotation axes, implying that joints have what has been called a ‘built-in mechanical play’ (cf. Kapandji, 1974). This ‘built-in mechanical play’ is generally dependent on joint position and potentially provides joints with more (or less) mechanical degrees of freedom than their primary axes of rotation would seem to suggest. These intra-articular positional changes during movements are described as translations and are part of normal joint kinematics. Optical stereophotogrammetry (SPG) studies (Bigliani, Kelkar, Flatow, Pollock, & Mow, 1996; Kelkar et al., 2001) have shown that the normal shoulder exhibits very small translations of the center of the humeral head during elevation in the scapular plane, and that tightening of the anterior capsular structures results in a posterior translation and a shift in glenoid contact when compared with untightened shoulders (Soslowsky, Flatow, Bigliani, & Mow, 1992). Furthermore, glenohumeral translations are more pronounced during active motions in positions where articular

conformity is low (Karduna, Williams, Williams, & Iannotti, 1997; Wuelker, Schmotzer, Thren, & Korell, 1994). In a study in which SPG was used to investigate the functional relations between the articular surface geometry, contact patterns, and kinematics of the glenohumeral joint, a larger-than-average incongruence in the shoulder joint was associated with larger anterio-inferior translation of the humeral head and an anterio-inferior shift of contact on the glenoid as a function of elevation angle (Kelkar et al., 2001). Translations of the glenohumeral joint decreased in all dimensions as the elevation angle of the shoulder increased from 0° to 90° and, conversely, translations increased as shoulder elevation increased from 90° to 180°. Congruence, a measure of the conformity between two surfaces, can be defined as the difference in the radii of curvature of the humeral head and the glenoid. The closer this difference is to zero, the more congruent is the joint. With the shoulder adducted there exists a slight glenohumeral mismatch. However, the joint becomes more congruent and thus the contact area of the humeral head on the glenoid increases as the shoulder is abducted (Warner et al., 1998). In general, in the shoulder, as in all other diarthrodial joints, the articular cartilage surface geometry (representing the structure) influences the contact areas and kinematics (representing the function) of the joint.

In the circular drawing task used in the present experiment, we expected articular conformity of the glenohumeral joint to be low at particular locations in the mid-sagittal plane where the task had to be performed. At these locations, or 'loose packed positions' (LPPs), articular conformity is low and the laxity of the capsule is often such that it allows a separation of the articular surfaces by an externally applied distractive force (Warwick & Williams, 1973). At which locations this was expected to take place is discussed next.

In the experiment (see Figure 1), the nine positions on the drawing surface formed a 3x3 matrix. Flexion/extension in both shoulder and elbow[1] were expected to be the primary direction of joint motion of the arm in the present circular drawing task at the nine positions in the sagittal plane with concomitant motions of the wrist joint in radioulnar direction. Articular conformity in the glenohumeral joint is low and the joint capsule is relatively lax when the arm is in a neutral flexion/extension position combined with a slight adduction. This is like positioning the arm in such a way that it allows the hand to rest comfortably in the lap when a person is seated, or when the arm is hung in a sling after a shoulder injury. Intra-articular translations are more prominent when the shoulder joint rotates in the vicinity of the resting position due to low glenohumeral conformity. These translations decrease in all dimensions as the elevation angle of the shoulder is increased from 0° to 90°.

[1] The shoulder mechanism consists of three synovial joints, i.e., the sternoclavicular joint, the acromioclavicular joint and the glenohumeral joint. The glenohumeral joint is usually referred to as the shoulder joint because it is the main contributor to joint rotations of the shoulder mechanism.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Elbow
Shoulder
C
Velocity excursion-time function
Velocity excursion (deg)
150
0
-150
D
Phase-time function
Phase (deg)
360
180
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E
Relative phase-time function
Relative phase (deg)
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150
120
90
60
0
5
10
15
Time (s)
Elbow/Shoulder

Figure 1.
Panel A. Schematic view of experimental setup. Participant is standing upright at the head of the drawing board (shown partially) with his or her trunk perpendicular to the drawing surface with a 10-cm minimum clearance of any part of the trunk and hips to the drawing board and holding a hand-filling round sponge. Nine white, self-adhesive round markers with a diameter of 1 cm (shown as numbers 1 to 9) indicate the nine different positions on the drawing surface. The numbers corresponding to positions (numbers 4 and 7) with low glenohumeral conformity are in blue. Seven infrared light emitting diodes (IREDs shown as red circles and numbered from 1 to 7) were attached to the dorsal surface of the hand and near joints of the wrist, elbow, shoulder, hip, knee and ankle on the right-hand side of the participant's body. OPTOTRAK system (not shown) is fixated at ceiling at distance of 2 m right of the participant. This OPTOTRAK system is facing downward at an angle of 35º relative to ceiling. IRED positions are measured in coordinate system that has Z-axis pointing orthogonal to (toward) projection screen, X-axis pointing parallel to screen, and Y-axis upward. Origin of this coordinate system is lower left corner of drawing board. Right-handed participant number 3 performs clockwise circular hand movements at position 5 in an audibly paced task at 1.0 Hz without visual control. Angular joint excursions were extracted off-line from the calculated positions of the five IREDs. The consecutive plots depict the angular excursion-time functions (panel B), the angular velocity-time functions (panel C) and the phase-time functions (panel D) of the elbow (blue plots) and shoulder (red plots) joint of the aforementioned 15-seconds trial. Next, panel E shows the continuous relative phase-time function between the elbow and shoulder joints (green plot).

We reasoned that by choosing a wide range of positions in the mid-sagittal plane in which the tasks were to be carried out, certain task conditions would be performed in the vicinity of the resting position of the shoulder. By constraining the task in the mid-sagittal plane of motion, a slight degree of adduction of the shoulder joint in positions 4 and 7 (see Figure 1) could be maintained, thereby allowing the shoulder to perform in a position associated with low articular conformity. However, neutral flexion/extension of the shoulder joint is best approximated with an arm posture in position 7. We therefore expected that position 7 and, to a lesser extent, position 4 would most likely be influenced by intra-articular translations that occur in the shoulder as a result of rotating the shoulder in areas with a low articular conformity. We expected that these positions would be associated with a decreased stability of shoulder-elbow coordination, as reflected by an increase in variability of the continuous relative phase.

Other determinants of inter-joint coordination stability

As stated above, the coupling of joints in the arm is partially effected by the stabilizing role of poly-articular muscles (e.g., biceps brachii acting as wrist supinator, elbow and shoulder flexor), by inertia (Lacquaniti & Soechting, 1982; van Bolhuis, van Gielen, & van Ingen Schenau, 1998), and by movement frequency (Dounskaia, Swinnen, Walter, Spaepen, & Verschueren, 1998; Kelso, Buchanan, & Wallace, 1991). It is by virtue of their spring-like properties that the coupling between neighboring joints is achieved by bi-articular muscles, thereby markedly influencing the organization of limb synergies (Gielen, van Ingen Schenau, Tax, & Theeuwen, 1990). Due to the inertia of the limb segments, angular motion at the wrist joint has

an impact on elbow and shoulder motion. If a torque is exerted at the shoulder or the elbow, it may result in an angular motion at the wrist and vice versa. However, the inertia of the hand is considerably less than that of the upper arm and forearm. Consequently, torques at the wrist will have less effect on the motion at more proximal joints (Soechting, 1984). Reaching out with the hand and thereby extending the arm in the mid-sagittal plane of motion increases the moments of inertia at the shoulder and elbow joints, which in turn, may also cause higher muscle-activity levels. Participants can anticipate these consequences and compensate for them during task performance (cf. Flanagan & Lolley, 2001). Hence, we did not expect the coordination stability to be systematically reduced between the shoulder and elbow joint pairs at more distant locations relative to the trunk.

Since earlier studies have shown that the elbow and wrist are loosely coupled (Lacquaniti, Ferrigno, Pedotti, Soechting, & Terzuolo, 1987), whereas the shoulder and elbow are tightly coupled (Lacquaniti, Soechting, & Terzuolo, 1986; Lacquaniti et al., 1987; Soechting, Lacquaniti, & Terzuolo, 1986), we decided to investigate the effects of movement speed on a loosely and a tightly coupled joint pair within the same effector system. To examine these effects, participants performed the circular drawing task at three different movement frequencies. In general, increased movement speed has been shown to destabilize certain coordination patterns of multi-joint arm movements. More specifically, Kelso et al. (1991) studied rhythmical unidirectional and bidirectional coordination of flexion and extension between the elbow and wrist joints of the right arm that were performed in the sagittal plane for two forearm positions: supine and prone. As cycling frequency increased, phase relations between the elbow and wrist joints only destabilized for the bidirectional coordination patterns. These observations support loss of stability as a central, self-organizing process underlying coordinative change. Also Dounskaia et al. (1998) have shown that increased frequency destabilizes certain coordination patterns of the loosely coupled elbow-wrist joint pair. In this study, unidirectional, bidirectional and free-wrist flexion/extension movement patterns of the elbow-wrist joint pair were analyzed across five cycling frequencies. Results provided evidence for two types of interactive torques exerted at the wrist: inertial torques arising from elbow motion and restraining torques arising from physical limits imposed on wrist rotation. The interactive torques were the primary source of wrist motion, whereas it appeared from the findings that the main function of wrist-muscle activity was to intervene with the interactive effects and to adjust the wrist movement to comply with the required coordination pattern. Furthermore, the unidirectional pattern was shown to be more in agreement with interactive effects than the bidirectional pattern, thus causing their differential difficulty at moderate cycling frequencies. However, when cycling frequency was further increased to 2.25 Hz, both the unidirectional and bidirectional movements lost their individual features and acquired features of the free-wrist pattern. These results suggest that multi-joint movement patterns that are more

in agreement with interaction effects can be maintained at higher speed levels than patterns requiring substantial muscular interference with the interactive torques.

In the present circular drawing task we expected overall relatively stable multi-joint movement patterns of the arm to emerge because the participants were free in choosing the size of the circle. On the other hand, we did expect higher movement frequencies to differentially affect the coordination stability of the contributing joint pairs. The rationale for this expectation was the following: (1) higher muscle-activity levels are required at higher frequencies to cope with interactive torques, and (2) active control requires timely processing of afferent feedback (Dounskaia et al., 1998). Consequently, we assumed that combined increases in muscle-activity levels and more rapid intervention of active control in movement because of increased frequency would only affect relatively unstable inter-joint coordination patterns. We expected the strong prime movers of the already tightly coupled shoulder-elbow joint pair to be able to comply with both requirements. Therefore, cycling frequency was not expected to affect the coordination stability of the shoulder-elbow joint pair. However, it was expected that the coordination stability of the loosely coupled elbow-wrist joint pair would decrease with increasing cycling frequency. Since coordination patterns at positions 4 and 7 of the shoulder-elbow joint pair were expected to be relatively unstable, we also expected coordination stability in positions 4 and 7 of the shoulder-elbow joint pair to decrease with increasing cycling frequency.

In sum, the rationale of the present study was as follows. We assumed that, in addition to the effects of bi-articular muscles in terms of joint coupling, a second important biomechanical factor, joint conformity, would also influence the coordination stability of both joint pairs differentially in circular drawing movements with the arm rotating at nine different locations in the mid-sagittal plane. Position-dependent variations of joint mobility were presumed whereby relatively unstable proximal inter-joint coordination should occur if the shoulder was moved in positions with low articular conformity (positions 4 and 7). Furthermore, we expected coordination stability only to decrease at these positions with increasing cycling frequency. Coordination stability for the loosely coupled distal joint pair was also expected to decrease at higher cycling frequencies. Inertia, however, was not expected to increase the stability of joint-interactions as the arm extended. The set-up also allowed us to assess the relative importance of joint conformity in graphic motor performance.

Method

Participants

Fourteen university students (five men and nine women) volunteered to participate. One participant failed to complete the experiment due to fatigue of the right

shoulder muscles. Another participant was excluded because of missing data during recording. The remaining participants (five men and seven women) were all right-handed. Their age ranged between 17.6 and 41.9 years (mean: 22.6) and none of them had motor problems. All participants gave their informed consent. They were rewarded for their participation with the option of course credits or payment. Experimental procedures were in accordance with the APA guidelines for the ethical treatment of human subjects.

Task and procedure

During the trials, the participants were standing upright at the head of the drawing board with their trunk perpendicular to the drawing surface with a 10-cm minimum clearance of any part of the trunk and hips to the drawing board (see Figure 1). The participants held a hand-filling round sponge in their right hand, with his or her fingertips around the sponge's circumference. The practically weightless sponge was wrapped in a polyethylene bag to minimize friction on the drawing board. Holding the sponge ensured a minimum involvement of fingers and thumb. The feet were placed slightly apart and with the toes 4 cm from the lower edge of the board to allow comfortable rotations to be made with the sponge in the free hanging right hand on the drawing surface. The board was 120 cm wide and 100 cm high, with a padded drawing surface of black imitation leather. Movements were paced by acoustic pacing signals at a frequency of 1.0, 1.5 and 2.0 Hz. The experimenter instructed the required rotational direction of the hand movements verbally (i.e., clockwise or counter-clockwise). Nine white, self-adhesive round markers with a diameter of 1 cm were used to indicate the nine different positions on the drawing surface (workspace). The positions were labeled 1-9 from the top position closest to the participant to the bottom, most distant position with horizontal and vertical inter-spaces of 10 cm. In all trial blocks, position cues were presented on a computer screen to aid the participants in determining the required starting locations. After assuming a comfortable position, the participant was asked to choose a location at shoulder height. This location was then marked as position 5 and taken as the center of the 3x3 matrix throughout the experiment (see Figure 1). Participants were free in choosing the size of the circles. Each block consisted of 54 trials based on every possible combination of imposed frequency, movement direction and imposed position. The conditions were counterbalanced in order to avoid confounding of order effects and separately randomized for each block. In a pilot study, the participants experienced visual hindrance by the drawing board that was positioned at close face-range in the mid-sagittal plane. They showed a tendency to bend their head sideways and lean over to the right. The tasks were therefore performed without visual control, that is, after having positioned the hand at the starting location for a particular trial, the participant was asked to close his or her eyes. We also carefully monitored the posture of the participants to ensure that they maintained a proper upright standing posture during trial execution. Per trial, the

experimenter started a 15-s recording period as soon as the participant had matched his or her movements to the imposed frequency.

Recording system

Movements were recorded at a rate of 100 Hz and with a spatial accuracy higher than 0.2 mm in *X, Y* and Z direction by means of a 3D-motion tracking system (Optotrak 3020). Seven infrared light emitting diodes (IREDs) were attached to the right-hand side of the participant's body at the following consecutive locations: the dorsal surface near the head of the fifth metacarpal bone (IRED-1), the styloid process of the ulna (IRED-2), the lateral epicondyle of the humerus (IRED-3), the acromion of the scapula (IRED-4), the anterior superior iliac spine (IRED-5), the lateral epicondyle of the femur (IRED-6), and the lateral malleolus of the fibula (IRED-7). IRED-1, mounted above the knuckle of the fifth metacarpal bone, was used to record the end-effector position.

Data analysis

All position data were filtered with a second-order Butterworth, zero phase lag, low-pass filter with a cut-off frequency of 8 Hz. For each 15-s trial the filtered end-effector trajectory, angles and angular velocities of shoulder, elbow and wrist joints were derived and visually inspected. To assess effects of practice and/or fatigue the 15-s recordings were divided by means of a computer-search procedure into a first, mid and last 5-s phase. The rotational directions (clockwise and counter-clockwise) were pooled in the data analyses since our main research question was focused on variations in the stability of inter-joint coordination as a function of the position and frequency task constraints.

Workspace kinematics

Frequency: Zero-crossings of the *Y* component of the end-effector position-time signal were determined to identify individual cycles. The mean cycle duration for the initial, middle and final 5-s phase of each trial was calculated and converted to a frequency unit (Hz).

Starting position: The first cycle of the *XY* end-effector position-time signal was isolated. The mean X-position and Y-position of this cycle was calculated separately for all conditions for all participants *(N* = 12). Next, the mean spatial variability (root-mean-square error) around the subsequent target positions for the corresponding *X* and *Y* starting positions was calculated.

Circle size: The peak-peak distance of the *X* and *Y* component of the end-effector position-time signal were obtained per cycle. From these data, the realized average circle size per trial was determined.

Circularity: The *X* and *Y* component of the position-time signals of the hand (IRED-1) were filtered with a second-order Butterworth, zero phase lag high-pass filter with a cut-off frequency of 0.5 Hz to eliminate within-trial positional drift. Assessment of the circularity of hand movements was based on the standard deviation (SD) of curvature in each cycle (see Verschueren, Swinnen, Cordo, & Dounskaia, 1999). The equation for the computation of curvature was

$$SdK = (x' y'' - x'' y') / (x'^2 + y'^2)^{3/2} \quad (1)$$

where x and y are the current coordinates on the end-point trajectory; x', y' and x", y" are the first and second time derivatives of x and y, respectively. In a circle, the curvature is constant at all times and the SD of curvature is zero. Accordingly, increases in the SD of curvature reflect distortions of circularity. The means of the SD of circularity (SdK) were computed per trial, and extreme outliers in the data were eliminated.

Plane-dependent angular displacements: The mean plane-dependent angular displacements of the shoulder (Mpdθ in °) were extracted off-line from the calculated positions of the third, fourth and fifth IRED. The Mpdθ expresses the plane-dependent contribution of the shoulder angular displacements to arm movements in the Cartesian coordinate system. Elevation was defined as the angle of the sagittal projection of the upper arm and a vector pointing forward through the trunk. Azimuth was defined as the angle of the projection of the upper arm in a horizontal plane relative to the forward direction and roll was defined as the angle of the projection in the fronto-parallel plane relative to the forward direction.

Kinematics

Plane independent angular rotations were extracted off-line from the calculated positions of the seven IREDs. The wrist, elbow, shoulder, hip and knee angles were defined as the enclosed angle between two neighboring limb segments.[2]

Decreasing angular rotations at the wrist joint indicate a radial abduction, 180° at the elbow joint indicates a full elbow extension. Increasing angular rotations at the shoulder and hip joints indicate a combined elevation/adduction/exorotation of the shoulder and a combined extension/abduction/exorotation of the hip. An angle of 180° at the knee joint indicates full knee extension. Anatomical joint space was

[2] In this footnote we present the code of the user defined Matlab v5.3 function of the enclosed angle.

```
% input: positions [xyz] of three joints (e.g., shoulder, elbow or wrist).
% output: enclosed angle (alfa) of the second joint.
function[alfa] = enclosed_angle(pos1,pos2,pos3);
vector 1 = pos1 - pos2; vector1 = vector1/norm(vector1);     % normalization to length 1
vector2 = pos3 - pos2; vector2 = vector2/norm(vector2);      % normalization to length 2
alfa = acos(dot(vector1',vector2')) * (180/pi);
```

defined as the three-dimensional joint space consisting of the radial/ulnar abduction of the wrist, the flexion/extension of the elbow, the combined elevation/adduction/exorotation and retroflexion/abduction/endorotation of the shoulder, the combined extension/abduction/exorotation and flexion/adduction/endorotation of the hip and the flexion/extension of the knee.

Joint amplitudes: The mean realized plane-independent angular displacements (MJθ in °) for all joint rotations were obtained per cycle from the position-time signal of each joint.

Relative phase

Continuous relative-phase time functions were inspected for branch cut crossings (phase wraps). No branch cut crossings were found.[3] The means (Mφ) and standard deviations (Sdφ) of the continuous relative-phase signals of the joint angle functions of the neighboring joints of the arm (wrist, elbow and shoulder) were calculated using Batschelet's (1981) procedure for circular statistics (see Meulenbroek, Thomassen, van Lieshout, & Swinnen, 1998).

Statistical evaluation

When relevant in the context of the presently formulated predictions, the dependent variables were evaluated by means of univariate analyses of variance (ANOVA). The within-subject factors were imposed frequency (1.0, 1.5 and 2.0 Hz), imposed position (nine positions) and movement direction (clockwise and counterclockwise). The Scheffé method (a = 0.05) was used for post-hoc comparisons of means.

Positions 4 and 7 (P47): To evaluate the effects of positions with low glenohumeral conformity, the means of the dependent variables at positions 4 and 7 were contrasted with the means of the dependent variables at the remaining seven positions where the task had to be performed. The results of these analyses will be reported under the factor P47.

[3] We decided to use cross-correlation measures between time functions of various joints to check for possible inconsistencies in our continuous relative phase assessments. Peak-peak detection and amplitude normalization may, in the case of noisy, low-amplitude signals yield a continuous relative phase signal with artificially high standard deviations. Such noisy signals should have resulted in unsystematic variations in the cross-correlation measures as a function of the experimental variables. Since cross-correlations proved to vary systematically as a function of the task variables and duplicated the results of the continuous relative phase signals, continuous relative phase was considered to be a reliable and representative measure of spatio-temporal inter-joint coordination.

Results

Task performance

Before assessing the variations in the stability of joint control across the three imposed frequencies and the nine imposed positions on the sagittal plane, we first verified whether the participants satisfied the imposed temporal and spatial constraints of the experimental task. In addition, effects of fatigue and/or practice were examined.

Realized frequency and realized positions

Throughout the three phases of a trial, the participants accurately produced the instructed movement frequencies (see Table 1). Consequently, practice and/or fatigue did not affect the realized frequencies. The mean spatial variability around the instructed target positions was 9.75 mm in the *X* and 9.90 mm in the *Y* dimension. Given the inter-target distance of neighboring targets of 100 mm, these results show that the imposed-position constraint of the experimental task was satisfied.

Table 1.
Means and standard deviations (between square brackets) of the realized frequencies during the initial, middle and final phase of trials for the three (1 Hz, 1.5 Hz, and 2 Hz) imposed frequencies pooled over the nine positions and both movement directions.

Realized Frequency	Imposed Frequency		
	1 Hz	1.5 Hz	2 Hz
Initial phase	1.03 [0.05]	1.53 [0.06]	2.01 [0.07]
Middle phase	1.02 [0.05]	1.52 [0.06]	2.00 [0.06]
Final phase	1.01 [0.05]	1.52 [0.06]	2.01 [0.07]

Circle size

Circle size varied between 106 mm at position 6 to 120 mm at position 5 (Table 2). A control analysis showed that the mean circle size pooled across positions 4 and 7 was not significantly different from the average realized circle size at the other positions ($F(1,11) = 2.60$, $p > 0.5$). As expected, higher cycling frequencies resulted in a scaling down of the circle sizes and vice versa (see Table 2).

Table 2.
Main effects of Orientation, Imposed Position and Frequency Mode (see text) on mean Circle Size, standard deviation of the curvature of hand movements (SdK) and the mean plane-dependent angular amplitudes of the shoulder joint (Mpdθ). Standard deviations of the dependent variables are added between square brackets.

Factor	Level	Circle Size	SdK	Mpdθ
Orientation	Roll			5.98 [3.71] *
	Elevation			13.75 [6.47]
	Azimuth			2.47 [1.39]
Imposed Position	1	114.65 [49.97]	0.021 [0.013] **	6.98 [6.74] *
	2	107.18 [49.42]	0.023 [0.015]	6.81 [5.71]
	3	113.54 [51.98]	0.023 [0.016]	8.47 [6.06]
	4	110.37 [50.43]	0.022 [0.013]	6.76 [6.66]
	5	120.45 [65.75]	0.021 [0.015]	7.29 [7.22]
	6	106.33 [49.29]	0.024 [0.015]	7.84 [5.60]
	7	119.70 [54.46]	0.021 [0.012]	7.42 [6.83]
	8	112.04 [57.60]	0.024 [0.015]	6.84 [6.35]
	9	117.03 [54.79]	0.023 [0.014]	8.19 [6.43]
Frequency Mode	1 Hz	133.73 [58.87]	0.020 [0.013] **	8.27 [7.17] **
	1.5 Hz	112.86 [57.27]	0.021 [0.013]	7.37 [6.73]
	2 Hz	93.84 [34.38]	0.027 [0.016]	6.57 [5.12]

* = p < .01, ** = p < .05

Thus, drawing circles under the task constraints of this experiment showed circle size to be relatively invariant in the sagittal plane of motion, was unaffected by positions 4 and 7, and displayed a tight frequency-to-amplitude relation.

Circularity

Figure 2 shows nine, two-dimensional plots of typical hand paths as realized in the experiment. The circular hand movements were performed by participant number three, in a clockwise direction at a frequency of 1 Hz. The figure demonstrates that perfect circles were almost never produced. We suggest that the distortion results from failure of the CNS to account for changes in anisotropy of viscosity and inertia (Pfann, Corcos, Moore, & Hasan, 2002).

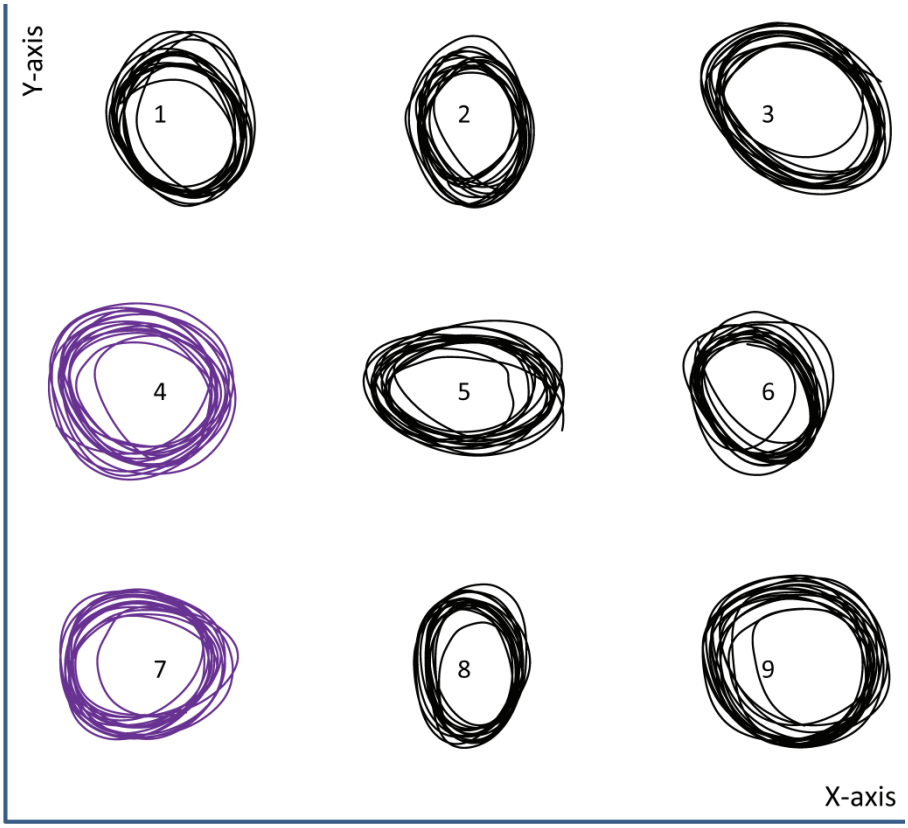

Figure 2.
Two-dimensional plots of circles and ellipses that were produced by participant number 3. The circles and ellipses were performed in a clockwise direction at a frequency rate of 1 Hz, without visual control, in the sagittal plane of motion. The locations of the plots coincide with the Imposed Positions (1 to 9; see Figure 1).

Deterioration of the circular hand movements was assessed by analyzing the standard deviation of the curvature of hand movements (SdK). Control analyses showed that the factor imposed position affected the SdK (see Table 2; $F(8,88) = 3.61$, $p < 0.05$). The SdK varied between 0.021 (positions 1, 5 and 7) and 0.024 (positions 6 and 8). Movement frequency displayed a significant effect on the SdK (see Table 2; $F(2,22) = 8.39$, $p < 0.05$); post-hoc analysis showed that the deterioration of the circular hand movements was significantly higher for the 2 Hz frequency mode than the lower frequency modes.

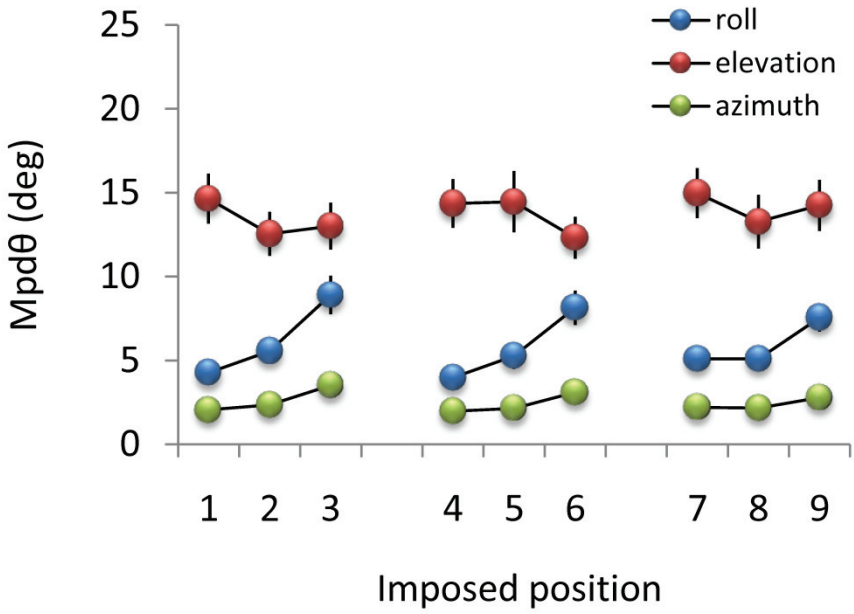

Figure 3.
Mean (plane-dependent) angular displacements in degrees in the roll, elevation and azimuth orientation, of the shoulder joint as a function of Imposed Positions (1 to 9; see Figure 1) for all participants (N=12). Error bars represent 95 % confidence intervals.

Plane dependent angular displacements

Control analyses showed that the mean plane-dependent angular displacements of the shoulder (Mpdθ in Table 2) varied strongly in the different planar dimensions ($F(2,22) = 55.20$, $p < 0.01$). Figure 3 displays the average angular displacements in the roll, elevation and azimuth direction of the shoulder joint as a function of posi-

tion. The effect of position (Table 2) was significant ($F(8,88) = 7.55$, $p < 0.01$). Post-hoc analysis showed that the displacements in the roll and azimuth direction were significantly higher in positions 3, 6 and 9 than in the other positions. The elevation remained relatively constant across the nine positions. Frequency also affected the displacements in the roll, elevation and azimuth orientation ($F(2,22) = 4.60$, $p < 0.05$; see Table 2). Post-hoc analysis for the roll displayed significantly higher displacements in the lowest frequency mode (1 Hz). For the elevation, all the three frequency modes were significantly different, displaying decreasing elevation with increasing frequency modes. Angular displacements in the azimuth orientation remained constant across the three frequency modes.Kinematics

Joint amplitudes

Table 3 shows the mean plane-independent angular displacements (MJθ in °) and mean realized frequency (MJF in Hz) for all joint rotations. The angular displacements at the shoulder and elbow were relatively large (10.82° and 17.95°) and small at the wrist, hip and knee (3.06°, 0.86° and 0.35°). The realized frequency and the variability of the frequency of the knee was relatively larger than the wrist, elbow, shoulder and hip.

Table 3.
Means and standard deviations of the plane-independent angular amplitudes (MJθ) and realized frequency (MJF) for all involved joints (wrist, elbow, shoulder, hip and knee). Standard deviations of the dependent variables are added between square brackets.

Joints	MJθ	MJF
Wrist	3.06 [2.16]	1.70 [0.44]
Elbow	17.95 [8.35]	1.52 [0.41]
Shoulder	10.82 [5.14]	1.52 [0.41]
Hip	0.86 [0.57]	1.49 [0.51]
Knee	0.35 [0.26]	2.30 [1.58]

Table 4.
Means and standard deviations of the plane-independent angular amplitudes (MJθ) of the hip joint for the nine (1 to 9) imposed positions. Standard deviations of the dependent variables are added between square brackets.

Hip	MJθ
Imposed Position	
1	0.74 [0.40]
2	0.86 [0.59]
3	0.93 [0.60]
4	0.77 [0.44]
5	0.83 [0.50]
6	0.93 [0.62]
7	0.79 [0.48]
8	0.86 [0.60]
9	1.03 [0.75]

Table 4 shows the mean plane-independent angular displacements (MJθ in °) of the hip as a function of position. The displacements at the hip increased systematically and were more variable as the participants reached out with their hand.

In the following control analyses we focused on the contributions of the wrist, elbow and shoulder angular displacements to the arm movements. The mean plane-independent angular displacements of the wrist, elbow and shoulder joints (MJθ in Table 5) varied strongly across the joints ($F(2,22) = 73.77$, $p < 0.01$).

Figure 4 displays the average wrist, elbow and shoulder displacements as a function of position in the workspace. The effect of position (Table 5) was significant ($F(8,88) = 12.15$, $p < 0.01$). Post-hoc analysis showed that wrist displacements remained constant across the nine positions. For the elbow, positions 3 and 9 showed significantly larger angular displacements than the other positions. For the shoulder, positions 4 and 7 showed significantly smaller displacements than the other positions.

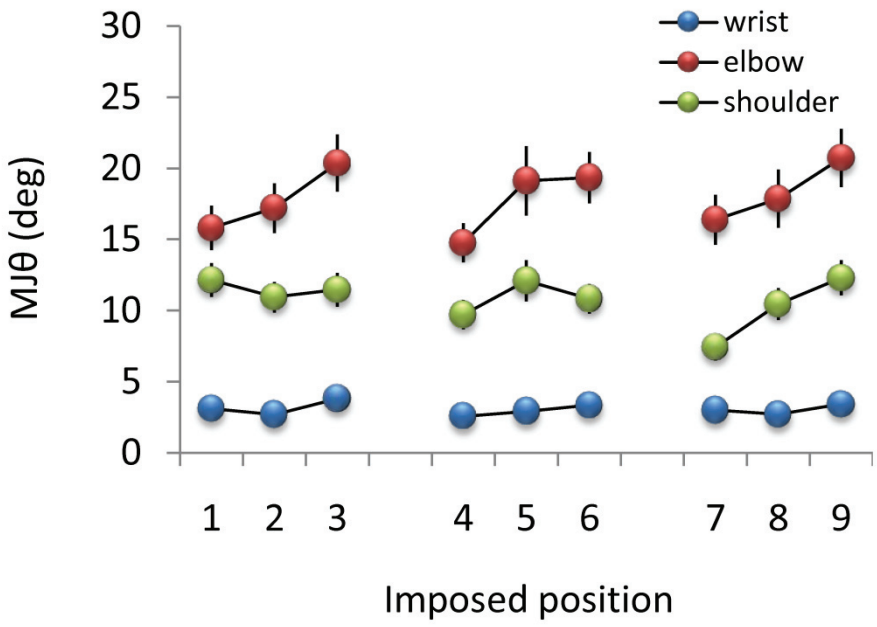

Figure 4.
Mean (plane-independent) angular displacements in degrees, of the wrist, elbow and shoulder as a function of Imposed Positions (1 to 9; see Figure 1) for all participants (N=12). Error bars represent 95 % confidence intervals.

This was confirmed by contrasting positions 4 and 7 with the remaining seven positions in the sagittal plane for the shoulder joint. The results showed that MJθ was significantly lower in these positions ($F(1,11) = 9.95$, $p < 0.05$). Frequency also affected the angular displacements ($F(2,22) = 5.00$, $p < 0.05$; see Table 5). Post-hoc analysis for the wrist displayed significantly lower angular displacements in the lowest frequency mode (1 Hz), whereas the opposite was true for the shoulder joint, which showed significantly higher displacements in the lowest frequency mode (1 Hz). For the elbow, all the three frequency modes were significantly different, displaying decreasing angular displacements with increasing frequency modes.

Table 5.
Main effects of Joints, Joint Pair, Imposed Position and Frequency Mode (see text) on the mean plane-independent angular amplitudes (MJθ), and mean (Mφ) and standard deviations (Sdφ) of continuous relative phase. Standard deviations of the dependent variables are added between square brackets.

Factor	Level	MJθ	Mϕ	Sdϕ
Joints	Wrist	3.06 [2.16] *		
	Elbow	17.95 [8.35]		
	Shoulder	10.82 [5.14]		
Joint Pair	Elbow/wrist		88.66 [116.06] **	43.93 [16.18] *
	Shoulder/elbow		130.17 [32.63]	12.43 [07.84]
Imposed Position	1	10.35 [7.35] *	106.10 [83.47]	26.79 [19.11]
	2	10.27 [7.90]	108.55 [88.92]	27.08 [20.06]
	3	11.88 [9.06]	121.54 [82.87]	25.91 [20.15]
	4	9.02 [6.67]	92.91 [90.52]	31.02 [20.07]
	5	11.37 [9.76]	108.02 [87.72]	27.36 [20.25]
	6	11.17 [8.47]	115.00 [80.51]	27.33 [21.77]
	7	8.94 [7.55]	103.52 [103.04]	32.65 [18.88]
	8	10.34 [8.56]	114.69 [85.10]	28.33 [20.47]
	9	12.15 [9.32]	114.44 [84.52]	27.14 [20.89]
Frequency Mode	1 Hz	11.79 [9.79] **	103.93 [88.98]	28.72 [20.70]
	1.5 Hz	10.59 [8.58]	103.88 [85.57]	28.84 [21.50]
	2 Hz	9.45 [6.32]	120.45 [87.71]	26.97 [18.40]

* = $p < .01$, ** = $p < .05$

Relative phase

Mean relative phase (Mφ)

Figure 5 displays Mφ for the elbow-wrist (distal) and shoulder-elbow (proximal) joint pair as a function of imposed position. An ANOVA with imposed position, imposed frequency, movement direction (clockwise and counter-clockwise) and joint pair (elbow-wrist and shoulder-elbow) as within-subject factors showed that the phase relations between both joint pairs differed significantly (see Table 5; $F(1,11) = 10.25$, $p < 0.05$). Position-independent relative phase relations for the distal joint pair amounted to ±90° and varied strongly across all positions. However phase

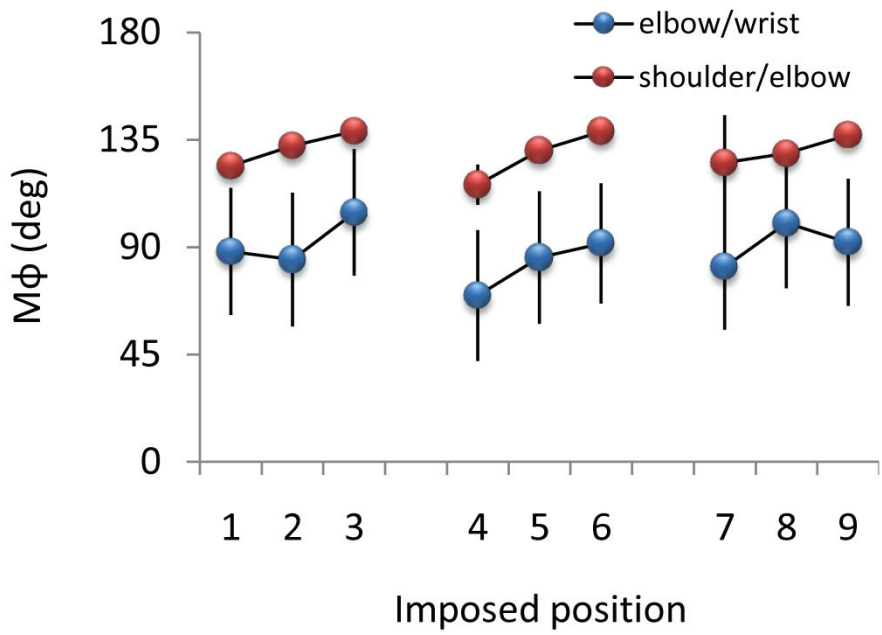

Figure 5.
Mean relative phase in degrees, of joint rotations as a function of Imposed Positions (1 to 9; see Figure 1) between the elbow-wrist (distal) and shoulder-elbow (proximal) joint pairs for all participants (N=12). Error bars represent 95 % confidence intervals.

relations for the proximal joint pair amounted to approximately 130° and increased systematically as participants reached out with their hand ($F(8,88) = 8.45$, $p < 0.01$). Movement frequency did not differentially affect phase relations of both joint pairs.

Standard deviation relative phase (Sdφ)

An ANOVA with imposed position, imposed frequency, movement direction (clockwise and counter-clockwise) and joint pair (elbow-wrist and shoulder-elbow) as within-subject factors showed that joint pair affected Sdφ (see Table 5). The distal joint pair displayed unstable phase relations amounting to ±45°, whereas Sdφ for the proximal joint pair approached ±12.5°, displaying more stable phase relations ($F(1,11) = 123.84$, $p < 0.01$). Imposed position (Table 5) showed a significant effect on the Sdφ of the two involved joint pairs ($F(8,88) = 3.29$, $p < 0.01$). Step-down analysis for the distal joint pair showed that the Sdφ was not affected by the factor position ($F(8,88) = 1.00$, $p > 0.05$) and displayed relative large variability at all positions (Figure 6).

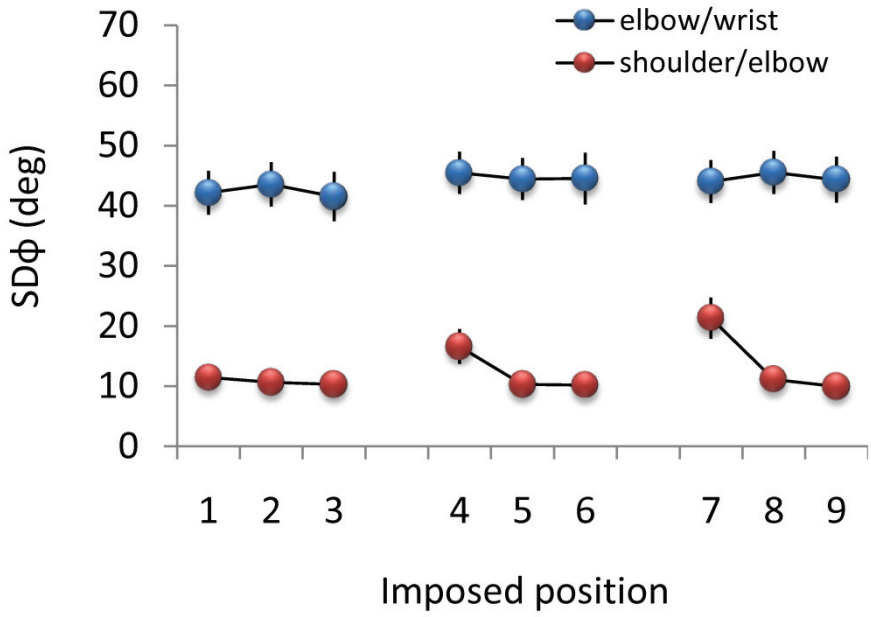

Figure 6.
Mean standard deviation of relative phase of joint rotations as a function of Imposed Positions (1 to 9; see Figure 1) between the elbow-wrist and shoulder-elbow joint pairs for all participants (N=12). Error bars represent 95 % confidence intervals.

The proximal joint pair showed position-dependent variations in Sdφ ($F(8,88) = 5.15$, $p < 0.01$) and the variability in Sdφ for this joint pair were consistently small except at positions 4 and 7. By contrasting positions 4 and 7 (P47) with the remaining seven positions in the sagittal plane we found a significant effect of P47 on Sdφ ($F(1,11) = 5.82$, $p < 0.05$). In step-down analyses for each joint pair separately, P47 showed a significant effect on Sdφ for the proximal joint pair only ($F(1,11) = 7.66$, $p < 0.05$). The disproportional effects of positions 4 and 7 on Sdφ for the proximal joint pair are shown in Figure 6. Post-hoc analyses showed that Sdφ of the nine positions for the proximal joint pair could be grouped into three subsets that differed significantly, viz. for position 4, position 7 and for the remaining seven positions in the sagittal plane. Imposed frequency affected Sdφ only marginally ($F(2,22) = 2.83$, $p < 0.10$). Also the effect of frequency on Sdφ for the distal joint pair was found to be marginal ($F(2,22) = 3.39$, $p < 0.10$).

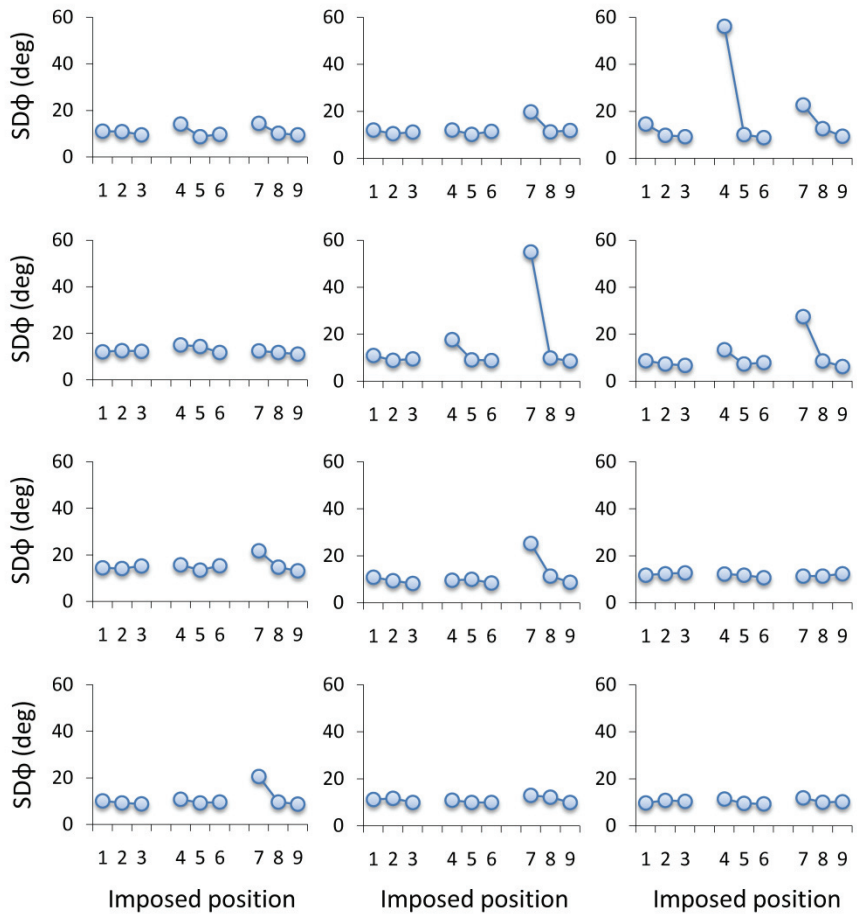

Figure 7.
Mean of the standard deviation of relative phase for all participants (N=12) between the shoulder-elbow (proximal) joint as a function of Imposed Positions (1 to 9; see Figure 1) per subject (pp 1 to pp 12).

Step-down analysis for the proximal joint pair revealed no significant effects of movement frequency on Sdφ ($F(2,22) = 1.09$, $p > 0.05$). Thus, drawing circles under the task constraints of this experiment showed variable, unstable and position-independent phase relations for the elbow-wrist joint pair and more stable position-dependent phase relations for the shoulder-elbow joint pair. The influence of positions 4 and 7 resulted only in disproportional unstable phase relations of the proximal joint pair. Movement frequency displayed non-linear marginal effects on the stability of the phase relations for the elbow-wrist joint pair, with relatively lower phase relations in the 2 Hz frequency mode.

Figure 7 displays Sdφ of the proximal joint pair as a function of the nine positions in the sagittal plane for all 12 participants. Across participants the proximal joint pair showed a relatively stable, position-dependent phase relation. However, with the exception of participant nine all participants showed disproportional distortions of the stable baseline profile at positions 4 and 7.

Discussion

In this study, we focused on the coordination of shoulder, elbow and wrist joints in circular drawing movements performed in the sagittal plane of motion. The aim was to assess the variations in the stability of joint control of articular rotation angles across three cycling frequencies and over a wide range of drawing positions in the sagittal plane. In performing the drawing task with the hand in the mid-sagittal plane of motion, the arm effectively possesses six degrees of freedom, whereas two functional degrees of freedom suffice for the task. The hand movements can be produced at all the investigated positions by primarily varying shoulder and elbow flexion/extension. Consequently, the arm system is overspecified and task-specific structural units (synergies) are created in joint space (Soechting et al., 1986). One may hypothesize therefore, that, at the level of movement planning, these structural units between joint rotations restrict the number of possible kinematic solutions (Greene, 1972). Meeting task demands in general requires the production of adequate hand-position changes by means of appropriate postural changes (Rosenbaum, Loukopoulos, Meulenbroek, Vaughan, & Engelbrecht, 1995). Positional changes in the shoulder coincide with intra-articular positional changes or translations in the shoulder joint (Soslowsky et al., 1992). However, the conformity between the humeral head and the glenoid is slightly mismatched in certain positions of the shoulder joint (Kelkar et al., 2001; Warner et al., 1998), while translations are more pronounced during active motions in positions where articular conformity is low (Karduna et al., 1997; Wuelker et al., 1994). The present findings indicate that these joint-surface characteristics induce position-dependent variations in the stability of joint interactions.

The analysis of the mean and standard deviations of relative phase confirmed that the coordination between shoulder and elbow (proximal joint couple) depended on drawing location (see Figure 1). Furthermore, the proximal joint couple showed overall a relatively stable phase relation, which was contained within a range of ±12° around a mean relative phase of ±130° and increased systematically as participants reached out with their hand (see Figures 6 and 7). In contrast, phase relations for the distal joint couple were position-independent and showed a large variability of ±44° with an average phase difference of ±90° (see Figures 6 and 7). These results are also in line with observations by Lacquaniti et al. (1987) supporting the view that the proximal joint pair generates the whole movement but corrections needed to fulfill the task requirements are generated at the distal joint pair.

Spatial effects on coordination stability

With the hand performing circular movements at nine different positions, positions 4 and 7 (see Figure 1), were of particular interest in this study. The configuration of the arm posture in these two hand positions was such that it allowed the shoulder joint to move in a position where glenohumeral conformity was low and where intra-articular translations between the head of the humerus and glenoid were more prominent. Phase relations of the proximal joint pair increased systematically as participants reached out with their hand with overall low variability at all positions, except positions 4 and 7 (see Figure 7), where the average variability was higher (±19°). This observation was characteristic for nearly all 12 participants even though individual shoulders varied in articular conformity (Kelkar et al., 2001).

Because the tasks were performed without visual control it could be argued that, increases in upright stance instability (Edwards, 1946; Travis, 1945) and increased amplitudes of natural oscillations of the body (Yoneda & Tokumasu, 1986) could have influenced the performance at the shoulder joint at positions 4 and 7. Our data indicated that the postural sway of the participants was multi-segmented (see Table 3; cf. Buchanan & Horak, 1999; McCullum & Leen, 1989). Because patients with vestibular complaints show excessive hip sway and center of gravity movement during clinical balance testing (Shupert, Horak, & Black, 1994), we assumed that hip excursions were indicative of trunk excursions. As Table 4 shows, the amplitudes of the hip excursions increased systematically and were more variable as the participants reached out with their hand. These observations imply that unstable phase relations at the proximal joint pair at positions 4 and 7 were not affected by increased amplitudes of natural oscillations of the body by performing the tasks without vision. Because the participants produced circular movements on a stationary surface, we assume that slight changes in contact force with the hand provided sensory cues about the direction of body sway, allowing attenuation of sway and enhanced control of upright stance (Jeka, Oie, Schoner, Dijkstra, & Henson, 1998; Jeka, Schöner, Dijkstra, Ribeiro, & Lackner, 1997; Rogers, Wardman, Lord, & Fitzpatrick, 2001).

It could also be argued that plane-dependent angular displacements in the roll, azimuth and elevation orientation of the shoulder at positions 4 and 7 were, on average, not comparable to the angular displacements at the remaining positions (Figure 3). This could account for differences in the stability of phase relations at the proximal joint pair. A control analysis, however, showed that angular displacements in the roll and azimuth direction of the shoulder in positions 3, 6 and 9 were higher than in the other positions, whereas shoulder elevation remained constant across the nine positions. This means that, except for positions 3, 6 and 9, plane-dependent angular displacements of the shoulder joint at the remaining positions were, on average, mutually comparable.

An additional artifact in our data could emerge from the fact that the biceps brachii muscle performs in a shortened state at positions 4 and 7. This could influence the fine tuning of this poly-articular muscle and affect the stability of the phase relations of the proximal joint pair at these two positions where average variability was ±19°. However, the biceps brachii performs in an even more shortened state at position 1, where the average variability of the phase relations was 11.45°. This observation militates against the possibility that the shortened state of the biceps brachia influenced the stability of the phase relations of the proximal joint pair at positions 4 and 7.

On the other hand, plane-independent angular displacements of the shoulder were found to be significantly lower at positions 4 and 7 than at other positions (see Figure 4). Interestingly, variations in the stability of phase relations for the proximal joint pair at positions 4 and 7 did not coincide with variations in phase relations. Consequently, coordinated behavior displays a surprising resilience, that is, it tends to maintain phase relations despite variations in joint mobility.

To assess the relative importance of joint conformity in graphic motor performance we will next discuss the possible effects of joint conformity of the shoulder joint on the coordination of the distal joint pair and on the deterioration of the circular hand movements. Phase relations and the stability of the phase relations of the distal joint pair remained unaffected by positional constraints, even in positions in which joint conformity of the glenohumeral joint were shown to be low. Furthermore, even though the standard deviation of the curvature, indicative of deterioration of the circular hand movements (see Verschueren et al., 1999), was shown to be position dependent, distortions of the circles and ellipses drawn by the hand in the sagittal plane indicating possible deviations from a circular motion, were not differentially affected by position 4 and 7. We can say conclusively that graphic motor performance is not affected by variations in joint mobility due to low glenohumeral conformity. This is presumably the case because: (1) the 'looseness' of the distal joint coupling overcomes effects of proximal joint variations, (2) proximal joint variations are 'filtered out' by adjusting limb stiffness (Van Galen & van Huygevoort, 2000) before they affect the distal joint pair or (3) proximal joint variations are actively compensated.

Inertial effects on coordination stability

Even though we did not analyze forces, we may speculate on the possible consequences of the presently demonstrated effects of joint conformity at the level of kinetics. In general, adjusting the position of body segments creates varying magnitudes of rotational inertia. An increase in the moment of inertia will result in an increase of moment of force (Adrian & Cooper, 1989). However, our results showed that the stability of the phase relations (Figure 6) did not increase systematically as the participants reached out with their hand. We presume that participants

were able to anticipate these consequences and to compensate for them during task performance (cf. Flanagan & Lolley, 2001). Thus, coordination stability for both joint pairs remained unchanged at locations that were more distant.

Frequency effects on coordination stability

By having participants move at various speeds (1, 1.5 and 2 Hz), we were able to examine the effects of movement frequency on a loosely and a tightly coupled joint pair being part of one and the same effector system. As expected, overall phase relations for both joint pairs were insensitive to variations in movement frequency. This was presumably the case because the participants were free in choosing the size of the circle, thereby allowing overall emerging movement patterns of the arm to be more in agreement with interaction effects (Dounskaia et al., 1998). As expected, the coordination stability of the tightly coupled shoulder-elbow joint pair was not affected by cycling frequency. However, contrary to expectations, higher cycling frequency did not decrease coordination stability in positions 4 and 7 of the proximal joint-pair where coordination stability was low. Such stable inter-joint coordination between the shoulder and elbow demonstrates the importance of a stable proximal base in the production of circular hand movements. Also contrary to expectations, the coordination stability of the loosely coupled distal joint pair displayed non-linear marginal effects and increased for higher cycling frequencies. The different effects of movement frequency on the loosely coupled distal joint pair and on the tightly coupled proximal joint pair as part of one and the same effector system generally supports the complementary nature of strategic and neuromuscular factors in sensorimotor coordination, in which haptic information may either stabilize or destabilize coordination dynamics (Kelso, Fink, DeLaplain, & Carson, 2001).

In sum, the production of circular movements in the sagittal plane of motion under the described task constraints was chiefly realized by sinusoidal movements in a relatively stable coupled proximal joint pair. The shoulder-elbow joint couple was predominantly exploited to meet the task demands in the sagittal plane where the stability of the joint interactions remained unaffected by increasing moments of inertia. The elbow and wrist joints showed a more variable dynamic relation, independent of movement frequency. The results of the present experiment provide evidence for the observation that the already tightly coupled shoulder-elbow joint pair, which is confined to the sagittal plane in circular hand movements, shows a tendency to maintain stable phase relations when the task is performed at high frequencies. However, the relatively stable joint-interactions between shoulder and elbow rotations break down because of perturbations from variations in joint mobility, arising from specific joint-surface characteristics at predicted locations in the sagittal plane.

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Chapter 3

Deliberate Control of Continuous Motor Performance

Abstract

This study was concerned with the means by which people vary movement parameters to satisfy more than one constraint at a time in a repetitive motor task. We expected that when people were simultaneously confronted with spatial and temporal constraints in an ellipse drawing task, they would either exploit the intrinsic amplitude-frequency relationships or activate less natural control regimes to prioritize their movement goals. By focusing on local amplitude and frequency errors and parameter changes from one movement to the next, we distinguished parameter changes reflecting exploitation of biomechanics from those requiring deliberate control. The findings demonstrate that at low movement speeds participants can pursue multiple movement goals simultaneously, but at higher speeds their capacity to satisfy multiple task goals is reduced. The method used here comprises a new way of inferring deliberate control from movement kinematics.

Introduction

Large-amplitude arm movements tend to be performed at low frequencies by means of shoulder and elbow rotations, whereas small-amplitude arm movements tend to be performed at higher frequencies by means of wrist and finger rotations (Rosenbaum, Slotta, Vaughan, & Plamondon, 1991; Vaughan, Rosenbaum, Diedrich, & Moore, 1996; Vaughan, Matson & Rosenbaum, 1998). Asking participants to depart from these movement patterns (e.g., to produce fast shoulder movements or slow wrist rotations), requires them to refrain from relying on intrinsic amplitude-frequency relationships and instead to activate less natural, possibly more attention-demanding, control regimes (cf. Zelaznik, Spencer & Ivry, 2002; Swinnen & Wenderoth, 2004). How do participants achieve such control?

To address this question, we studied the continuous drawing of ellipses (see also Meulenbroek, Thomassen Van Lieshout & Swinnen, 1998; Meulenbroek, Bouwhuisen, Thomassen & Rosenbaum, 1999; Thomassen & Meulenbroek, 1998). Subjects were supposed to match the amplitudes and frequencies of their movements to target values that varied from trial to trial. Our predictions about the way the ellipses would be controlled were based on known biomechanical inter-dependencies between movement amplitude and frequency (Kay, Kelso, Saltzman & Schoner, 1987; Rosenbaum et al., 1991). The predictions can be understood by consulting Figure 1.

The center of Figure 1 shows a hypothetical goal amplitude-frequency combination. Around the centrally located goal-parameter combination are eight categories of possible performance errors. Single-parameter errors are shown on the *x* and *y* axes, whereas double-parameter errors (i.e., errors in both amplitude and frequency) are depicted in the four quadrants. Figure 1 also shows a hypothetical series of attempts to reduce the errors from one movement to the next in response to performance error. In the depicted case, the initial error is an amplitude that is too short (A^-) and a frequency that is too high (F^+). The error-reduction process is represented by a sequence of four arrows.

Let movement *i* be a single loop of particular amplitude and frequency. Various outcomes are possible for movement *i* + 1. One possibility is that both the amplitude and frequency of movement *i* + 1 are identical to those of movement *i*. By contrast, one or both of the parameters of movement *i* + 1 differ from those of movement *i*, in which case one of three outcomes is possible:

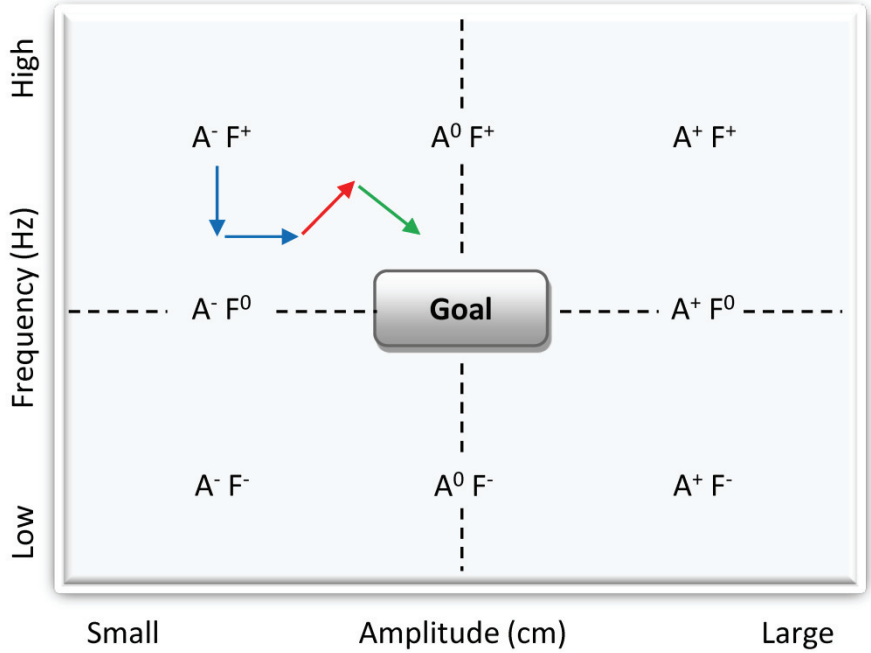

Figure 1.
Possible changes in performance in successive trials. Eight categories of possible performance errors are shown with respect to the goal amplitude-frequency combination, shown at the center. Single-parameter errors ($A^{+}F^{0}$, $A^{0}F^{+}$, $A^{-}F^{0}$, and $A^{0}F^{-}$) correspond to the positive and negative directions of the dashed x (Amplitude) and y (Frequency) axes. Double-parameter errors ($A^{+}F^{+}$, $A^{-}F^{+}$, $A^{-}F^{-}$, and $A^{+}F^{-}$) correspond to the four possible combinations of positive and negative directions of Amplitude and Frequency. The sequence of arrows towards the goal-parameter combination depicts a hypothetical series of transitions in Amplitude-Frequency space, beginning with an amplitude that is too short (A^{-}) and a frequency that is too high (F^{+}) relative to the goal. The first blue arrow pointing downward represents a single parameter change in the frequency domain, the second blue arrow pointing rightward represents a single parameter change in the amplitude domain, the third red arrow represents a double parameter change, and the fourth green arrow indicates a quasi-double parameter change (see text).

Either the amplitude or the frequency of movement $i + 1$ differs from that of movement i. In both cases, we speak of a *single parameter change*. The amplitude of movement $i + 1$ increases and the frequency of movement $i + 1$ decreases, or the amplitude of movement $i + 1$ decreases and the frequency of movement $i + 1$ increases. In both cases two parameters change, but the participant may have intentionally changed only one parameter and the other parameter may have changed passively on the basis of the natural relationship between amplitude and frequency. We call such changes *quasi-double parameter changes*.

Both the amplitude and frequency of movement $i + 1$ increase or decrease. Here we speak of intentionally driven *double-parameter changes* because the combined changes defy the natural, biomechanical relationship between the two parameters (i.e., the inverse relation between frequency and amplitude).

A final important aspect of the transition is whether the parameter changes from movement i to $i + 1$ do or do not reduce the error relative to the instructed amplitude and frequency. Each of the above changes can be classified as being successful (smaller error) or not (larger error or no reduction in error).

By scrutinizing the amplitude and frequency errors and subsequently determining the incidence and size of single, double, and quasi-double parameter-error changes as well as the success of such changes, we sought to identify those movement-parameter adjustments that were primarily due to deliberate attempts by the participant to meet the task goal. We assumed that double parameter changes were deliberate because they defy the biomechanically given inverse relation between amplitude and frequency. Therefore, we predicted that there would be an appreciable number of such changes and that there would be more of them when the required tempo of movement was slow than when it was fast because deliberate control takes time and is more likely to be manifested when there is time for it to operate. Additionally, we expected that in low-speed conditions, double parameter changes would occur most often when local errors consisted of combined amplitude and frequency overshoots or undershoots. The reason for this prediction was that double-parameter changes would provide the most efficient means of error reduction, and at low speeds the deliberate control required to achieve such efficient error reduction would be easier than at high speeds.[4]

Method

Participants

Twelve right handed adults (six male and six female) participated. Their mean age in years and months was 24;9 (range: 14;6). All participants had normal hearing and normal or corrected-to-normal vision. None had motor problems. All participants gave their informed consent and received course credits or payment. Experimental procedures followed the APA guidelines for the ethical treatment of human participants.

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[4] Our predictions would not have been confirmed if (a) participants would produce more double parameter changes when the required tempo of movement was fast than when the required tempo of movement was slow, or (b) in high-speed conditions, double parameter changes would occur most frequently when local errors consisted of combined amplitude and frequency overshoots or undershoots.

Task and Procedure

Before the experiment began, the participant was given written instructions and was asked to write his or her name on a normal sheet of white paper. The orientation at which the participant spontaneously positioned the sheet on the writing surface was used to align a rectangular projection area (25 by 20 cm) that was displayed on the writing surface by means of a Liquid-Crystal-Display (LCD) video and a surface mirror, both positioned under the writing table. A translucent surface (30 × 25 cm) was built into the writing table to allow for rear (or bottom) projection of the display.

The bottom of the projection area (closest to the participant) served as the orientation of the baseline of writing during the entire 90-minute experiment. Before the experiment began, the translations of the tip of the pen onto the *x* and *y* dimensions of the graphic workspace were calibrated in a separate recording of the position and orientation of the rectangular projection area which the participant indicated a preference for the graphic workspace. For this purpose, a 3D rigid co-ordinate frame was used. Following the reference recordings, the participant was asked to adopt a comfortable writing posture. The experiment consisted of 100 trials and was self paced. The participant wrote on a 6 cm-height paper strip which s/he was asked to unroll by pulling leftwards between trials (see Figure 2). Before a trial started, the computer controlling the experiment and the data storage sent a signal to a host computer that controlled the display of the visible writing pattern and the presentation of the acoustic stimulus. First, the complete writing pattern was displayed on the writing surface by means of the LCD video. The pattern was clearly visible and consisted of a series of 12 loops generated by means of Hollerbach's (1981) coupled-oscillator algorithm. The loop pattern approximated a normal cursive writing trace with a slant of approximately 70 deg and was generated on the basis of sinusoidal vertical and horizontal position changes combined with a constant rightward progression. The loop pattern's height was either 3, 6, 9, 12, or 15 mm. The corresponding widths were 3.5, 7.0, 10.5, 14.0, or 17.5 mm. Because subjects generally write at a frequency of approximately 5 Hz when asked to write at high speeds (Teulings & Maarse, 1984), we decided to impose movement frequencies of either 1, 2, 3, 4, or 5 Hz.

Pilot recordings showed that subjects found it difficult to lock their writing movements onto a moving cursor when the cursor moved at a frequency of 5 Hz. Therefore, we added an additional pacing signal which we thought would help subjects realize the required movement frequencies.

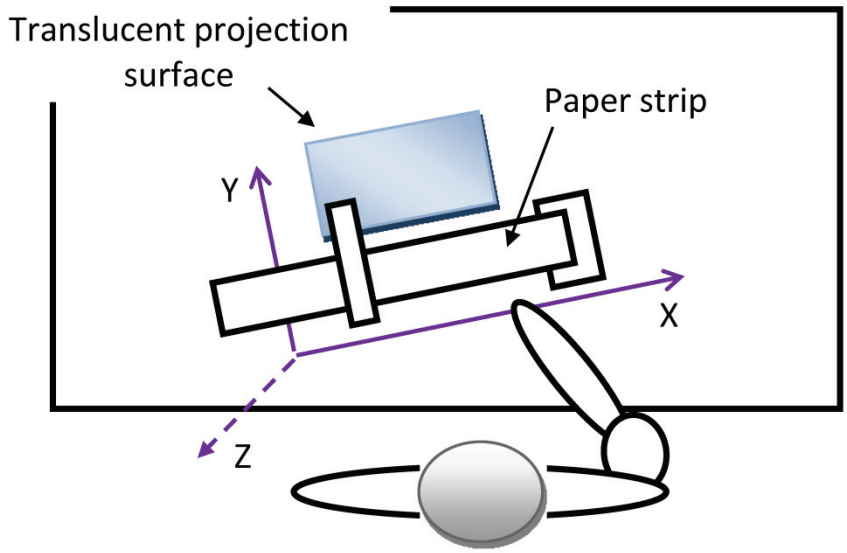

Figure 2.
Top-view of the experimental set-up. The participant sat comfortably at the writing table. In front of the participant a rectangular projection area (25 by 20 cm) was displayed onto the writing surface by means of a Liquid-Crystal-Display (LCD) video and a surface mirror, both positioned below the writing table. A translucent surface (30 × 25 cm) was built into the writing table for this purpose. The participants wrote on a paper strip (height: 6 cm) which he/she was asked to unroll by pulling leftwards between trials.

Because acoustic stimuli are processed more quickly than visual ones, we also decided to present, in synchrony with the moving cursor, an acoustic signal that changed sinusoidally in intensity (between approximately 60 and 70 dB; tone pitch 400 Hz). The intensity change of the acoustic pacing signal was mapped onto the vertical displacements of the moving cursor. As the cursor moved up, the acoustic signal's intensity increased, and as the cursor moved down, the signal's intensity decreased. To our knowledge, no previous studies have used such externally paced handwriting.

After the participant inspected the stimulus pattern, s/he verbally indicated to the experimenter that s/he was ready to perform the next trial. A trial consisted of three phases. During the first phase, which lasted 5 s, the cursor moved along the ellipse and the acoustic pacing signal sounded. During the second phase, the acoustic pacing signal was turned off for a single cycle of the moving cursor. During the third and final phase, the acoustic pacing signal was reintroduced and the cursor started to move rightward along the stimulus loop pattern. The cursor was projected such that it was clearly visible to the participant. Watching the cursor and simultaneously

written trace did not require significant eye or head movements. Participants were asked to copy the pattern by following the moving cursor and trying to reflect its position as accurately as possible. A trial ended when the cursor moved through 12 loops. Movements were recorded throughout the trial. Each of the 25 amplitude-frequency combinations was replicated four times, resulting in a total of 100 trials. Amplitude-frequency conditions changed after a block of four replications. Half the participants were given a sequence in which amplitudes and frequencies increased in successive trials. The other half of the participants were given a sequence in which amplitudes and frequencies decreased in successive trials.

Recording System

One rigid body, consisting of three infrared light emitting diodes (IREDs) fixated at a 1 × 1 × 1 cm inter-IRED distance on a flat aluminum plate was mounted on the top of the barrel of a normal ballpoint pen (Bouwhuisen, Meulenbroek & Thomassen, 2002). Translations and rotations of the rigid body were recorded at a rate of 100 Hz and with a spatial accuracy higher than 0.2 mm in the x and y direction by means of a 3D-motion tracking system (Optotrak 3020, Northern Digital Inc., Waterloo, Canada). The position and orientation of the rigid body were transformed to the position of the pen tip.

Data Analysis

The digitized pen-tip displacement signals in the x and y directions were filtered with a second-order, dual-pass Butterworth filter. The high-pass frequency was 0.5 Hz for all signals, which eliminated the movement components related to the low-speed rightward progression component of the movements. The low-pass cut-off frequency of the filter was set to twice the pacing frequency of the condition in which the signal was recorded. This ensured that an automatic peak-valley detection algorithm could be applied reliably to each position-time signal. On the basis of this algorithm, successive cycles were extracted by means of a peak-peak detection algorithm (Hollerbach, 1981; Meulenbroek et al., 1996). Describing successive cycles by their peak-amplitude and frequency allowed us to quantify the biomechanically and non-biomechanically induced relationships between movement amplitude and frequency.

For each obtained movement cycle, the realized amplitude was calculated for the detrended x and y-position time signals separately. Then the amplitude in the horizontal and in the vertical dimension was averaged to obtain a local cycle amplitude, A, expressed in mm. A similar procedure was applied to arrive at a local cycle frequency, F, expressed in Hz. Next, the parameters A and F were used to calculate the local spatial error, A_{err}, expressed as a percentage of the instructed amplitude, where positive values reflected amplitude overshoots and negative amplitudes reflected amplitude undershoots. Similarly, the local frequency error,

$F_{err,}$ was expressed as a percentage of the instructed frequency, where positive values reflected higher than instructed frequencies and negative values represented lower than instructed frequencies. Thus, A_{err} and F_{err} reflected the signed relative amplitude and frequency errors, respectively, given the instructed amplitude and frequency values conveyed by the moving cursor.

The next step concerned quantifying the error changes from one movement to the next. Except from the first movement cycle in each trial, we obtained for each cycle, the two parameters ΔA_{err} and $\Delta F_{err,}$ where ΔA_{err} equalled A_{err} of cycle *i* minus A_{err} of cycle *i*-1*, and* ΔF_{err} equalled F_{err} of cycle *i* minus F_{err} of cycle *i*-1.

A minimum value, *d*, set at 1% of the local instructed parameter value, was used to identify a change in parameter value. Any absolute value greater than or equal to this value qualified as a parameter-value change.[5]

To test our predictions, we first categorized the A_{err} and F_{err} data into the eight classes indicated on the axes and in the quadrant centers of Figure 1. These eight categories represented all possible combinations of overshoots and undershoots in the amplitude and frequency domain. Subsequently, each ΔA_{err} and ΔF_{err} combination, representing the error change realized from one movement to the next, was classified as a single-parameter change or as a quasi-double parameter change or as a double-parameter change.

Sign tests were used to evaluate the statistical significance of observed differences between the incidences of movement-error categories. Sign tests were also used to evaluate the incidence of the categories of parameter changes. These non-parametric tests were more conservative than Chi-square tests in this context. We used paired samples t-tests to evaluate the statistical significance of the size of the observed movement errors and parameter changes. Bonferroni corrections were applied whenever multiple tests were conducted.

Results

The results will be presented as follows. First, we will report the incidence and size of the observed amplitude and frequency errors. Second, we will present the incidence and size of single, double, and quasi-double parameter changes from one movement to the next, collapsed over the five speed conditions of the experiment. Third and finally, we will evaluate the study's main prediction that double parameter

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[5] Even though this conservative minimum value may have resulted in an overestimation of the incidence of intended parameter changes, we were careful to test the core hypothesis concerning task-constraint prioritization by comparing data that were independent of threshold variations. In fact, various minimum values were tested, but the results of these analyses all pointed in the same direction as presently reported in relation to the 1% criterion.

changes would occur most frequently when the required tempo of movement was slow.

Amplitude and Frequency Errors

In total, 51,555 movement cycles were evaluated with respect to the realized amplitude and frequency relative to the goal amplitude and frequency and with respect to the realized parameter change from one movement to the next.

Table 1.
Incidence of Amplitude and Frequency Errors expressed as percentage of the local goal parameter. Positive values represent parameter overshoots whereas negative reflect parameter undershoots. Note the central cell represents the absence of any error.

		Amplitude		
		Too Small	*No error*	*Too Large*
Frequency	*Too High*	29.74% (F_{err} = + 7 % ; A_{err} = -22 %)	1.12% (F_{err} = + 7 %)	11.40% (F_{err} = + 7 % ; A_{err} = +19 %)
	No Error	9.66% (A_{err} = -21 %)	0.33%	4.18% (A_{err} = +20 %)
	Too Low	27.65% (F_{err} = - 8 % ; A_{err} = -21 %)	1.25% (F_{err} = - 8 %)	14.67% (F_{err} = - 8 % ; A_{err} = +19 %)

The cells in Table 1 are arranged in a 3 × 3 matrix and show the incidence of the eight categories of possible performance errors collapsed over the five instructed-amplitude and five instructed-frequency conditions. The mean sizes of the errors are specified in parentheses. At the center of Table 1 is the number of movements for which both the amplitude and frequency were on target. Note that this number is low, as expected, because of the stringent criterion we used to identify errors and error changes (i.e., 1% of each of the two goal parameters, see Method section and Note 2).

Incidence. All participants produced more amplitude undershoots than amplitude overshoots (sign test, N=12, $p < .001$). The incidence of positive (42.26%) and negative (43.56%) frequency errors proved statistically indistinguishable (sign test, N=12, ns).

Size. The size of the amplitude errors ($\underline{M}$ = 20.61 %, $\underline{SD}$ = 4.73%) was, on average, almost three times the size of the frequency errors ($\underline{M}$ = 7.61%, $\underline{SD}$ = 1.78%, $t(11) = 10.01$, $p < .001$), suggesting that participants were more tolerant of amplitude errors than frequency errors. However, the size of the amplitude overshoots ($\underline{M}$ = 19.21 %, $\underline{SD}$ = 4.12%) was statistically indistinguishable from the size of the

amplitude undershoots (M = 22.01%, SD = 7.12%; t (11) = 1.44, ns). Similarly, the positive and negative frequency errors were statistically indistinguishable (M = 7.34%, SD = 2.17% and M = 7.88%, SD = 2.14%; t (11) = 0.77, respectively; ns).

Figure 3 (page 63) shows the time course of the size of the first seven unsigned (top panel) and first seven signed (bottom panel) parameter errors. To avoid clutter, this figure only includes data from error categories with an incidence higher than 5%. The figure shows that the mean size of the amplitude and frequency error decreased sharply over the first movement cycle and then continued to decrease gradually over subsequent movement cycles. Amplitude errors were, on average, almost three times larger than frequency errors. These observations were comparable within each of the five shown error categories (bottom panel). A control analysis of between-trial error reduction revealed that off-line parameter changes were restricted to movement amplitude and in these cases these error reductions were considerably smaller than within-trial performance improvements.

Figure 4 (page 64) shows trial-to-trial changes in performance that were realized off-line (i.e., between trials). The amplitude error for low (1 Hz and 2 Hz) and medium (3 Hz) movement speeds were larger in the first trial (j) than in subsequent trials within the same block ($j + 1$, $j + 2$ and $j + 3$). At high movement speeds (4 Hz and 5 Hz) the amplitude error did not decrease between trials. At low movement speeds the amplitude error was gradually reduced between trials j, $j + 1$, and $j + 2$, and at medium movement speed between trials j and $j + 1$. In contrast, the frequency error was only reduced between trials j and $j + 1$ if the participants moved slowly (low movement speed).

Parameter Changes from one Movement to the next

Table 2 (page 65) shows the three types of parameter changes (single, double and quasi-double) as a function of the three categories of error changes (increase, decrease, and increase and decrease) expressed as a percentage of the local goal parameter. The mean sizes of the parameter changes (ΔF_{err} and ΔA_{err}) are specified in parentheses. Details concerning the table follow.

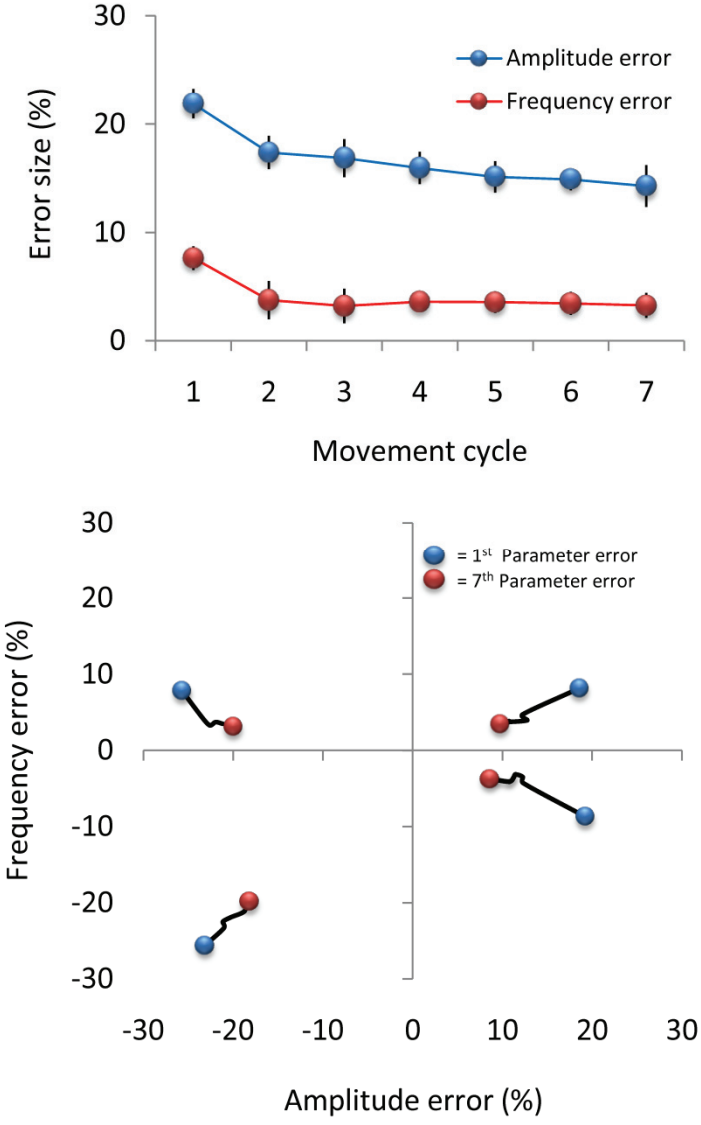

Figure 3.
Time course of the mean error size (in percentages) of the first seven unsigned (top panel) and signed (bottom panel) parameter errors (amplitude and frequency). Error bars (top panel) represent SD. Blue circles (bottom panel) indicate the 1st combined parameter error and the red circles indicate the 7th combined parameter error.

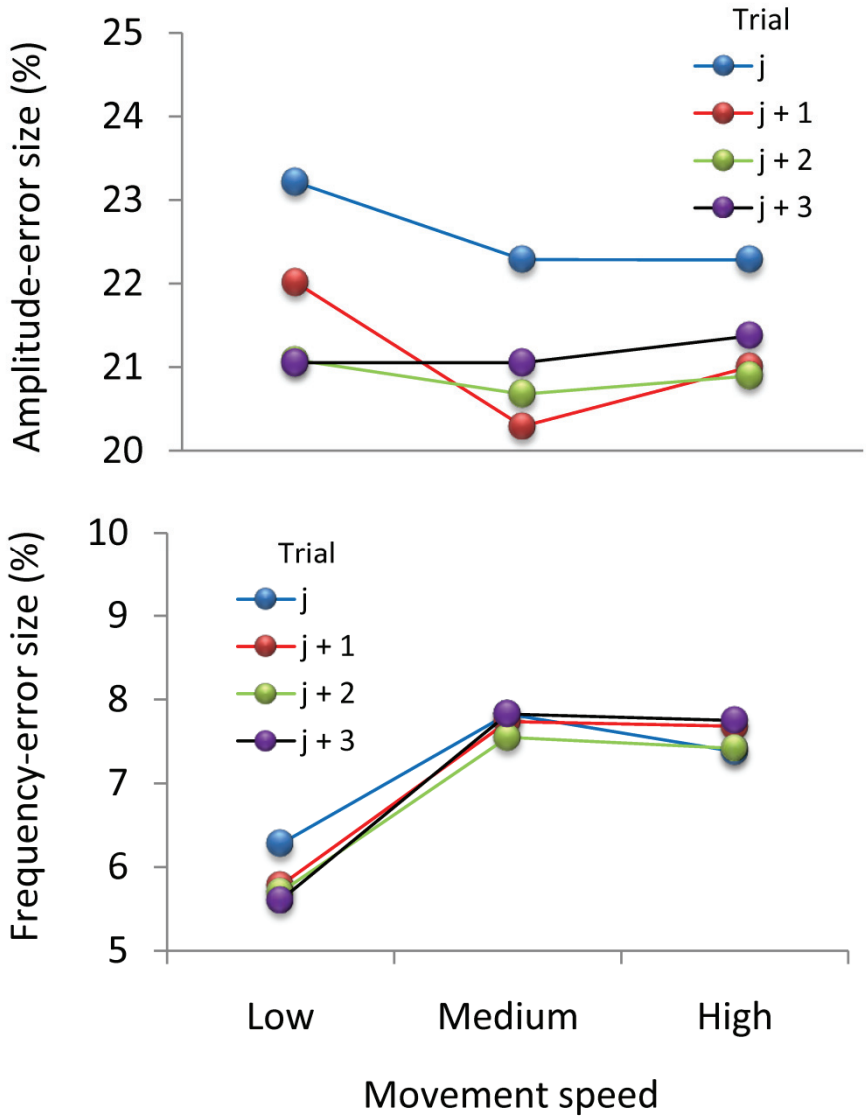

Figure 4.
Trial-to-trial changes in performance realized between trials j, j + 1, j + 2 and j + 3. The top panel shows the mean amplitude-error size (in percentages) at low (1 Hz and 2 Hz), medium (3 Hz) and high (4 Hz and 5 Hz) speed. The bottom panel shows the mean frequency-error size (in percentages) at low (1 Hz and 2 Hz), medium (3 Hz) and high (4 Hz and 5 Hz) speed.

Table 2.
Incidence of Parameter Changes (Single, Double and Quasi-double) as a function of the three categories of error changes (Increase, Increase & Decrease, and Decrease) expressed as percentage of the local goal parameter. The mean size of the parameter changes (ΔF_{err} and ΔA_{err}) are specified in parentheses.

		Type of parameter change			
		Single	*Double*	*Quasi-Double*	**Total**
Error change	*Increase*	9.97% (ΔF_{err} = 1 % ; ΔA_{err} = 6 %)	4.48% (ΔF_{err} = 5 % ; ΔA_{err} = 8 %)	8.10% (ΔF_{err} = 6 % ; ΔA_{err} = 9 %)	**22.55%** (ΔF_{err} = 4 % ; ΔA_{err} = 8 %)
	Increase & Decrease	14.36% (ΔF_{err} = 2 % ; ΔA_{err} = 7 %)	16.01% (ΔF_{err} = 6 % ; ΔA_{err} = 8 %)	18.04% (ΔF_{err} = 6 % ; ΔA_{err} = 10 %)	**48.41%** (ΔF_{err} = 4 % ; ΔA_{err} = 8 %)
	Decrease	2.31% (ΔF_{err} = 1 % ; ΔA_{err} = 9 %)	9.59% (ΔF_{err} = 6 % ; ΔA_{err} = 8 %)	15.23% (ΔF_{err} = 7 % ; ΔA_{err} = 10 %)	**27.12%** (ΔF_{err} = 4 % ; ΔA_{err} = 9 %)
	Total	**26.64%** (ΔF_{err} = 1 % ; ΔA_{err} = 7 %)	**30.08%** (ΔF_{err} = 6 % ; ΔA_{err} = 8 %)	**41.37%** (ΔF_{err} = 6 % ; ΔA_{err} = 9 %)	**98.08%** (ΔF_{err} = 4 % ; ΔA_{err} = 8 %)

Incidence. In general, participants obeyed the task instructions by trying to satisfy both the requested amplitude and frequency constraints. From one movement to the next they succeeded in changing the local movement parameters toward the goal movement parameters. Thus, all participants produced more movements that reduced either one or both parameter error(s) than movements that caused both local movement parameters to drift away from the goal parameter combination (sign test, N=12, $p < .001$).

Size. On average, the errors in amplitude changes (M = 8.10%, SD = 0.70%) were larger than the errors in frequency changes (M = 4.27%, SD = 0.37%; t (11) = 19.17, $p < .001$). Even though the size difference was small, the outcome fits with the observation that participants had a much larger tolerance for amplitude errors than for frequency errors. Consequently, the parameter range left for improvement was larger for amplitude than for frequency. Furthermore, the size of the amplitude changes that reduced the error (M = 8.35%, SD = 0.76%) was on average larger than the amplitude changes that increased the error (M = 7.59%, SD = 0.64%), t (11) = 7.42, $p < .001$. Also the size of error reducing frequency changes (M = 4.44%, SD = 0.38%) was on average larger than the error increasing frequency changes (M = 3.93%, SD = 0.43%), t (11) = 5.18, $p < .001$.

Single, Double, and Quasi-Double Parameter Changes

Incidence. As expected, an appreciable number of the moment-to-moment changes in performance were double-parameter changes (30.08%; see Table 2). While single and double parameter changes were statistically indistinguishable (sign test, N=12, ns), all 12 participants produced more quasi-double parameter changes (41.37%) than double parameter changes (30.08%), (sign test, N=12, $p < .001$) or single-parameter changes (26.64%), (sign test, N=12, $p < .001$).

Size. On average, the amplitude changes in the quasi-double parameter changes (M = 9.32%, SD = 0.83%) were significantly larger than the amplitude changes in the double-parameter change (M = 8.03 %, SD = 0.62%; t (11) = 9.67, p < .001) and in the single-parameter change (M = 6.95%, SD = 0.91%; t (11) = 10.30, p < .001). Moreover, the amplitude changes in the single-parameter changes were larger than in the double-parameter changes (t (11) = 2.99, p < .001). Also the size of the frequency change in the quasi-double parameter changes (M = 6.11 %, SD = 0.49%) was, on average, significantly larger than the frequency change in the double-parameter changes (M = 5.64%, SD = 0.47%; t (11) = 11.06, p < .001) and single-parameter changes (M = 1.05%, SD = 0.25%; t (11) = 38.60, p < .001). Finally, the mean size of the frequency change of the double-parameter was significantly larger than the mean size of the frequency change of the single-parameter changes (t (11) = 39.81, p < .001).

Single, Double, and Quasi-Double Parameter Changes as a Function of Movement Speed

Incidence. The top panel in Figure 5 shows the incidence of the single, quasi-double, and double parameter changes as a function of movement speed. The percentages of the quasi-double (37.83%) and double (42.56%) parameter changes at the lowest movement speed were statistically indistinguishable (sign test, N=12, ns.) while for all participants both quasi-double and double parameter changes occurred more often than the single-parameter changes (18.62%), (sign test, N=12, p < .001). As expected, all 12 participants produced more quasi-double changes (49.42%) than double changes (29.92%), (sign test, N=12, p < .001) or single parameter changes (19.34%), (sign test, N=12, p < .001) in the 2-Hz mode. Eleven of the twelve participants produced more double than single-parameter changes (sign test, N=12, p < .05) in the 2-Hz mode. In the 3-Hz mode the percentages of the single (26.31%) and double-parameter change (28.14%) were statistically indistinguishable (sign test, N=12, ns.) but were both lower than the quasi-double parameter changes (sign test, N=12, p < .001) for all 12 participants. In the 4-Hz mode the incidence of the double-parameter change (25.76%) was lower for 11 of the 12 participants than the single parameter change (32.32%), (sign test, N=12, p < .05) and lower, for all 12 participants, than the quasi-double parameter change (39.57%), (sign test, N=12, p < .001), while the incidence of the single and quasi-double parameter changes were statistically indistinguishable (sign test, N=12, ns.).

The results at the highest movement speed were comparable to those for the 4-Hz mode. All twelve participants produced fewer double-parameter changes (24.00%) than single (36.61%), (sign test, N=12, p < .001) or quasi-double (36.48%), (sign test, N=12, p < .001) parameter changes, while the percentages of the single and

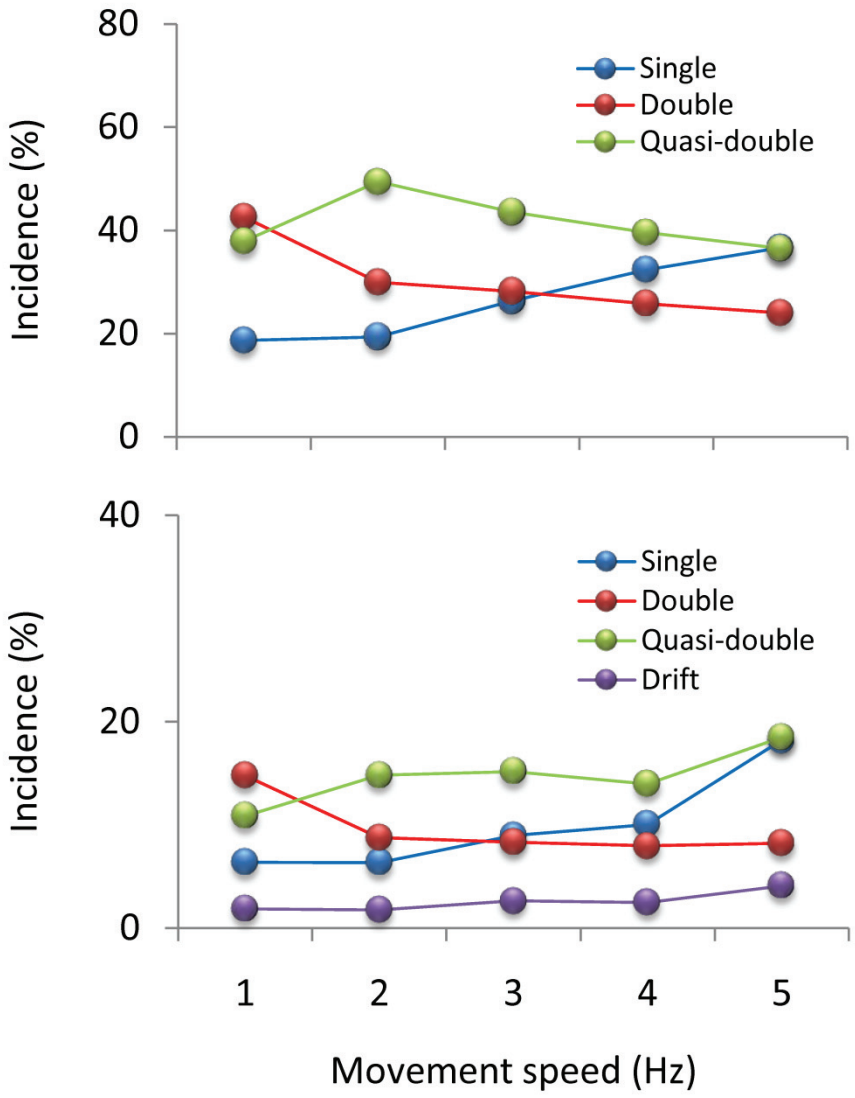

Figure 5.
Incidence (in percentages) of single, double and quasi-double parameter changes as a function of movement speed (1 Hz, 2 Hz, 3 Hz, 4 Hz and 5 Hz). Top panel: all data. Bottom panel: single parameter changes (single), double parameter changes that decreased the error (double), double parameter changes that increased the error (drift), and quasi-double parameter changes (quasi-double) for the subset of the data that accommodated for possible data contaminations due to exploitation of the biomechanical relationship between amplitude and frequency.

quasi-double parameter changes were statistically indistinguishable at the highest movement speed (sign test, N=12, ns.).

The bottom panel of Figure 5, finally, shows the incidence of various types of parameter changes that immediately followed $A^{+}F^{+}$ and $A^{-}F^{-}$ performance errors. The reason for isolating this subset of the data is that the parameter changes that followed these errors were not due solely to natural biomechanical tendencies. In other words, the double parameter changes under these conditions were considered to reflect deliberate control. The bottom panel of Figure 5 shows the incidence of the single parameter changes, double parameter changes that reduced both the amplitude and frequency error (double), double parameter changes that *increased* both the amplitude and frequency error (which we have labeled drift), and quasi-double parameter changes. As expected, double parameter changes that reduced both the amplitude and frequency error at the lowest tempo (1 Hz) outnumbered the other parameter changes. More specifically, the incidence of the double parameter changes (14.75%) at the lowest tempo was higher for 10 of the 12 participants than the incidence of the quasi-double parameter changes (10.85%), (sign test, N=12, $p < .05$) and higher for all 12 participants than single (6.35%), (sign test, N=12, $p < .001$) and drift (1.84%, (sign test, N=12, $p < .001$). For all 12 participants quasi-double parameter changes outnumbered both single (sign test, N=12, $p < .001$) and drift (sign test, N=12, $p < .001$) parameter changes, and single parameter changes outnumbered drift changes (sign test, N=12, $p < .001$. In contrast, in the 5 Hz mode, quasi-double (18.45%) and single (18.20%) parameter changes were statistically indistinguishable, while both parameter changes outnumbered double (8.19%), (sign test, N=12, $p < .001$) and drift (4.09%), (sign test, N=12, $p < .001$) parameter changes, with 11 of the 12 participants producing more double parameter changes than drift (sign test, N=12, $p < .05$).

Discussion

This study was concerned with the means by which people vary parameters of movement relevant to achievement of a task goal. The principal aim was to distinguish parameter changes that reflected the exploitation of biomechanics from those that required deliberate control to override natural biomechanical tendencies. To pursue this distinction, we examined the extent to which people can satisfy more than one constraint at a time in a repetitive motor task. We expected that when people were simultaneously confronted with spatial and temporal constraints in an ellipse drawing task, they would either exploit the intrinsic amplitude-frequency relationships or refrain from relying on these intrinsic relationships to prioritize their movement goals. By focusing on individual local amplitude and frequency errors and parameter changes from one movement to the next, we sought to distinguish parameter changes that reflected the exploitation of biomechanics from those that required deliberate control. Pursuing this logic, we found that the most movements

(41.37%) were quasi-double parameter changes and, as such, can be said to have resulted from exploiting (or following) natural biomechanical tendencies. The high incidence of such changes is, of course, consistent with Bernstein's (1967) influential view that adaptive motor behavior entails exploitation of, rather than resistance to, physics. Fewer movements (26.64%) resulted from single parameter changes. Most important for this study, an appreciable number of movements were double parameter changes (30.08%; Table 2), which we took to reflect deliberate control because the resulting movements entailed overriding natural amplitude-frequency relationships.

That the relative frequencies of the different kinds of parameter changes reflected strategic influences was supported by the dependence of the parameter changes on movement speed. As seen in the top panel of Figure 5, at low movement speed (1 Hz), participants could produce double-parameter changes as often as quasi-double parameter changes, with single parameter changes occurring the least often. By contrast, at high movement speed (5 Hz), when deliberate control was presumably harder, participants produced more single and quasi-double parameter changes than double parameter changes. These results confirm our prediction that double movement parameter changes would outnumber the other parameter changes at low movement speed (bottom panel in Figure 5) and that quasi-double and single parameter changes would outnumber double parameter changes at higher movement speeds.

How successful were the observed parameter changes? As reported above, participants produced more movements that reduced either one or both parameter error(s) than movements that led to both local movement parameters drifting away from the goal parameter combination (75.53% versus 22.55%). Moreover, early in the trials, errors were large, but the size of the error was substantially reduced over subsequent movements (Figure 3). Amplitude errors were, on average, almost three times larger than frequency errors, and the ratio between both errors remained approximately constant over movement cycles. These observations indicate that participants were more tolerant of amplitude errors than of frequency errors, perhaps because of differences in acuity for the two kinds of signals. The difference between frequency and amplitude errors could also be associated with a competition for visual-motor resources (i.e., processing information about the cursor position and using that information to control the limb).

Furthermore, as regards movement amplitude, participants typically produced more undershoots than overshoots, reminiscent of other smaller-than-required amplitudes in studies of aiming and possibly indicative of a strategy in which participants gradually decreased the percentage of undershoots and "sneaked up" on the target as part of a "play-it-safe" approach (see Engelbrecht, Berthier, & O'Sullivan, 2003; Elliott, Hansen, Mendoza, & Tremblay, 2004). This strategy of "sneaking-up" on the target corresponds to the notion of attempting to reduce travel costs in movement

(see Rosenbaum et al., 1995, for further discussion and simulations). Relatedly, a control analysis of between-trial error reduction revealed that participants mainly realized off-line parameter changes at lower movement speeds and chiefly to movement amplitude (see Figure 4). In these cases the error reductions were considerably smaller than within-trial performance improvements.

Is deliberate control required to do what is unnatural? While it is tempting to suppose that an act of will is needed to initiate a gait whose frequency departs from the walking eigenfrequency or to begin oscillating the two index fingers at a relative phase other than 0° and 180°, spontaneous variation might account for such departures from natural values, making it unclear whether the departures are statistical oddities rather than deliberate choices. Our strategy in focusing on the control of two variables at once (amplitude and frequency) gives us a way of approaching this difficult problem. Because the two variables we have studied have a natural, inverse, relation, changes that violate the natural relation are unlikely to be due to chance alone. Indeed, the likelihood of both variables changing in some joint fashion is given by the product of their probabilities if the changes are independent. The likelihood can be even smaller if the pairwise, unnatural changes are dependent. Furthermore, if the changes occur when they are adaptive for goal attainment, it is hard to imagine that they are not the result of deliberate control (although difficulty of imagination hardly constitutes proof). Nonetheless, assuming that deliberate control occurred in our task, such control presumably reflected internal representations of factors that are important to govern (Rosenbaum, Meulenbroek, Vaughan, & Jansen, 2001; Swinnen & Wenderoth, 2004).

A final remark is that this work offers a new way of determining when deliberate control comes into play vis à vis traditional methods used in cognitive psychology. The traditional method, from Posner and Snyder (1975), is to measure reaction time to detect stimuli that are known to be likely but which are miscued or only symbolically cued by immediately preceding signals. Subjects in such experiments can direct their attention at will to consciously expected locations. In those experiments, deliberate control is inferred from reaction times and errors in tasks that are mainly perceptual. The present study offers a new way of inferring deliberate control from kinematics in tasks that are mainly motoric.

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Chapter 4

Joint-action Coordination of Redundant Force Contributions in a Virtual Lifting Task

Abstract

In this study we investigated redundancy control in joint action. Ten subject-pairs (dyads) performed a virtual lifting task in which isometric forces needed to be generated with two or four hands. The participants were not allowed to communicate but received continuous visual feedback of their performance. When the task had to be performed with four hands, participants were confronted with a redundant situation and between-hand force synergies could, in principle, be formed. Performance timing, success rates, cross-correlations and relative-phase analyses of the force-time functions were scrutinized to analyze such task-dependent synergies. The results show that even though the dyads performed the task slower and less synchronized in the joint than in the solo conditions, the success rates in these conditions were identical. Moreover, correlation and relative-phase analyses demonstrated that, as expected, the dyads formed between-subject synergies that were indicative of force-sharing in redundant task conditions.

Introduction

One of the key challenges of cognitive neuroscience is to understand the principles that govern redundancy control, i.e., how biological systems extract from a large set of available control dimensions the minimum number of dimensions that is needed to act adequately. The issue was first addressed by Bernstein (1967) who in studies of multi-joint task performance identified "the degrees of freedom problem". Since then a variety of mechanisms have been demonstrated by means of which people 'solve' redundant control problems. For example, the coupling of actuators into motor synergies is one strategy to simplify coordination problems (Cole & Abbs, 1986; Santello, Flanders & Soechting, 1998; D'Avella, Saltiel & Bizzi, 2003; Ivanenko, Grasso, Zago, Molinari, Scivoletto, Castellano, Macellari & Lacquaniti, 2003). For single-actuator movements it has been suggested that the central nervous system uses motion plans that are defined in terms of joint angles (Uno, Kawato & Suzuki, 1989; Nakano, Imamizu, Osu, Uno, Gomi, Yoshioka & Kawato, 1999; Rosenbaum Loukopoulos, Meulenbroek, Vaughan & Engelbrecht, 1995; Rosenbaum, Meulenbroek, Vaughan & Jansen, 2001) or hand-position coordinates (Morasso, 1981; Flash & Hogan, 1985; Viviani & Flash; 1995). Combined with, respectively, the minimum torque-change and minimum jerk principles the neuromotor system is supposed to solve the redundancy problem quasi-automatically. Regardless of the nature of the reference systems in which the preparation of hand displacements takes place at various levels of the neuromotor system, experiments have shown that movements are always planned in such a way that the execution of these plans is robust against the variability that is inherent to the motor system (Harris, 1998; Harris & Wolpert, 1998).

Because lifting an object together requires the cooperation of two people it is an attractive task to study coordination in joint task performance. First, it allows us to determine the extent to which joint-action coordination is reactive or proactive. In addition, it allows us to investigate how groups deal with redundancy. How multiple degrees of freedom are contained in joint-action situations has hardly been studied before and we reasoned that a controlled study of a virtual joint-lifting task could fill this gap. Before going into the details of the experimental task we designed for this purpose, we first summarize what is known on redundancy control in complex task performance by individuals.

Intrapersonal coordination

During static and dynamic force-production tasks, individual finger forces show signs of mutual dependence. For example, when a person is asked to exert force with a single digit, force occurs at other digits as well (enslaving effect; for a review see Schieber & Santello, 2004). Also when a person exerts maximal force with two

fingers simultaneously, the total force produced by the two fingers is smaller than the sum of the maximal force production of both fingers separately (force-deficit effects; see Li, Latash & Zatsiorsky, 1998; Danion, Schoner, Latash, Li, Scholz & Zatsiorsky, 2003). These force-deficit effects of finger coordination resemble the well-known phenomenon of bilateral deficit (Koh, Grabiner & Clough, 1993; Oda & Moritani, 1994, 1995; Hakkinen, Kraemer & Newton, 1997). Findings in split-brain patients (Gazzaniga & Sperry, 1966), cortical lesions (Wyke, 1971) and of reduction of EMG after TMS of the motor cortex (Ferbert, Priori, Rothwell, Day, Colebatch & Marsden, 1992) suggest that, for simultaneous movements and dual-task performance by the individual, bilateral interhemispheric inhibition mediated through interhemispheric fibers plays some role in reducing motor performance, as indicated by measurements such as movement initiation, force and speed (Ohtsuki, 1994). Furthermore, systematic covariations between finger forces indicate that the coupling of fingers into motor synergies is an important control strategy for isometric force production of the digits of one hand. For example, Santello and Soechting (2000) investigated the control of full-hand grasping by measuring finger-contact forces when subjects lifted, held, and replaced a manipulandum. They showed that there are two basic temporal synergies in the control of isometric forces by the digits of the hand: one in which the forces of all of the digits vary to comparable degrees in the same direction, i.e., in phase, and a second, in which the forces exerted by some of the fingers are 180° out of phase with the forces exerted by other fingers. The first synergy suggests the presence of a "common drive" to all of the extrinsic finger muscles and is presumed to suit coarse control of forces, whereas the second one suggests a finer “force-stabilizing” control strategy (see also Li et al., 1998). In the present study we were concerned with characterizing the coordination of finger forces that are in operation when *two* people perform a force production task together.

Interpersonal coordination

Needless to mention is, as the proverb says “Many hands make light work”, that there are situations conceivable in which joint action is compulsory for obvious reasons, e.g. when the to-be-lifted object is too heavy or its dimensions are too awkward to be handled alone. Otherwise, group members acting together are, in general, at a disadvantage when compared to actions carried out by an individual. In particular, it has been shown that performance is seriously hampered in joint action if the task at hand requires individuals to time their actions contingent upon those of others (Burstedt, Edin & Johansson, 1997; Schmidt, Bienvenu, Fitzpatrick & Amazeen, 1998; Knoblich & Jordan; 2003).

Burstedt et al. (1997) investigated the coordination of fingertip forces when two subjects (i.e. a dyad) lifted one object as compared to when this task was carried out unimanually or bi-manually by a single subject. Even though grasp stability was

accomplished in a similar manner, synchronizing the actions of the fingertips of two subjects remained poor in comparison to performance by a single subject, even after practice. Also force generation, prior to lifting the object, was executed slower by two subjects (723 ms) than bimanual (459 ms) and unimanual (456 ms) performance by one subject. Likewise, replacing the object after the "replace" command was given, was carried out more slowly in trials involving two subjects, notwithstanding the observation that the trial was always performed successfully.

Both joint and single action can, in principle, rely on the same control mechanisms. Research conducted on rhythmic tasks has shown that the same dynamical fundamentals that govern the coordination of the movements of the limbs of individuals also govern the coordination of rhythmic movements of dyads who share visual information of their performance (Schmidt, Carello & Turvey, 1990; Schmidt & Turvey, 1994; Amazeen, Schmidt & Turvey, 1995). Even though the preferred inter-personal coordination regimes were weaker than intra-personal between-limb coordination (Schmidt et al., 1998), these studies nevertheless showed that group members clearly tend to synchronize their actions when they can see each other's movements.

A different approach to model synchronized action coordination between individuals is to propose that subjects (actors) plan and execute their actions in relation to what they anticipate the partner will do. Knoblich and Jordan (2003) have shown that groups indeed possess the ability to use and learn an anticipatory coordination strategy based on visual information even when they encounter more coordination problems than individuals due to increasing task demands. However, groups were able to enhance their performance if they were provided an external cue regarding the state of the partner's action alternative. Although the availability of such information did not affect performance initially, group performance became more similar to individual performance in later trials.

Experimental Paradigm and Predictions

We developed an isometric-force virtual lifting task with real-time feedback that allowed us to assess joint-action coordination under redundant task conditions. Our virtual lifting task (see Figure 1 top panel) was performed by subjects individually (solos) or in pairs (dyads) who were asked to generate isometric forces. The task consisted of generating an upward pressure with the left and right index finger on load cell transducers (lifting phase) after which these forces needed to be stabilized and maintained for a two-second period (holding phase). The aim of our study was to contrast control mechanisms of intra-personal and inter-personal coordination and focus on essential features of force sharing in a lifting task.

Fast haptic feedback loops from tactile afferents of the fingertips (~65 ms; Johansson & Birznieks, 2004) with which individuals or dyads applied pressure on

both sensors allowed them to monitor force modulations of their own contribution to the task. Individuals could also rely on relative slow online visual feedback (~135 ms; Carlton, 1981, Saunders & Knill, 2003) of the bar displacements on the computer screen to perceive the consequences of their actions. Dyads, however, only received relative slow online visual feedback of their partners' actions, no haptic feedback (see Rosenbaum et al., 2006 for reverse conditions). We therefore expected between-limb intra-personal coordination to be stronger than inter-personal coordination regimes resulting in enhanced performance in controlling the tilt of the bar. Even though we expected proactive coordination in joint action to be weaker than in single action, as has been demonstrated by Schmidt et al. (1998), our prediction implies that the coupling of effectors into task specific units would be informationally based.

In performing the isometric lifting task with four hands, i.e. when the system was overspecified, dyads received fast haptic feedback of their own contribution to the task and only relative slow online visual feedback of the consequences of the actions they jointly brought about. In these redundant conditions, however, the output to the lifting task was composed of both actors' actions thereby masking the individual contribution to the task. This means that actions carried out by one partner were not directly observable for the other. A viable way for the actors to anticipate and execute their actions based on visual feedback of the composite movements of their joint action is for the partners to adapt to the dynamics of these composed (superimposed) movements. The way that partners can learn about the dynamics of the joint-contribution to the task is by forming an internal model of the joint-dynamics of the action of which they are part of (cf. Atkeson, 1989; Jordan, 1994). Conditt, Gandolfo and Mussa-Ivaldi (1997) have demonstrated the presence of adaptive processes in the control of multijoint arm movements in point-to-point reaching movements in a velocity-dependent force field. They suggested that adaptation to a novel force field occurs by creating an ''internal model'' of this field. We expected actors to adapt to the dynamics of their joint contribution as expressed by increasing stable interactions of balancing the bar and we therefore took systematic covariations between the redundant (supernumerary) force-producing hands in redundant joint-action conditions to reflect between-subject synergies that are brought about by adaptive processes in sharing the task.

Method

Participants

Twenty right handed students (4 male and 16 female) from the University of Nijmegen participated. Handedness was determined using a modified version of the Edinburgh Handedness Inventory (Oldfield, 1971). Their mean age in years and months was 22;4 (in years; months - range: 15;11; SD: 3;3). All participants had

normal hearing and normal or corrected-to-normal vision and none had motor problems. All participants gave their informed consent. They were rewarded for their participation with either course credits or payment of 12 Euros. Experimental procedures followed the APA guidelines for the ethical treatment of human participants.

Apparatus

To perform the experimental task, the participants were randomly paired and were seated comfortably on adjustable chairs at opposing ends of the setup, vis-à-vis, at freestanding tables that were separated by a solid freestanding screen (see Figure 1 top panel). The virtual lifting task was displayed on two 17" CRT monitors (refresh rate: 75 Hz; 1024 by 768 pixels) that were placed at eye-level and at a comfortable distance on the table squarely in front of each participant. Two load cell transducers were mounted upside-down on the edge of each table and interspaced at 20 cm. Force applied to the load cell resulted in changes of the electrical resistance of strain gauges housed in the load cell transducer (type BC302, DS Europe, Italy). The output from the load cell was amplified with a low-drift instrumentation amplifier and sampled in epochs starting from stimulus onset and ending 6000 ms later at 1500 Hz. Force data from sensors 1 & 3 and force data from sensors 2 & 4 were linked by calculating the sum of the force output. The paired force data sets were resampled (at 75 Hz), smoothed and amplified with a gain of 375. The resampled data served as displacement data for the left (sensors 1&3) and right (sensors 2&4) end of the bar and were recorded. The duration of the entire loop of the resampled data from one measurement to the next was 13.33 ms and the time-lag between force input and drawing the bar on the display was on average 2.70 ms. A zero force measurement just before the start of the experiment was obtained to calibrate the zero point.

Task

The participants were not allowed to communicate in any way but they received real-time visual feedback of the lifting task that was presented on their display. On these displays a black colored rectangular object (bar) was displayed resting on a horizontal baseline (see Figure 1 bottom panel). Bar movements on one of the displays were mirror imaged, thereby mimicking a real-life joint lifting task.

Participants could control the amount of lift (vertical position) and the tilt (rotation) of the bar in the frontal plane by exerting an upward pressure with their left and right index finger on load cell transducers. By distributing the applied force evenly over the load cell transducers they could ensure that the bar remained horizontally orientated. The amount of force required to lift the bar into the target area was similar whether the task was executed with one, two or four hands. By keeping the

target force constant across all conditions we complied with the "Many hands make light work" principle.

Procedure

Before the experiment started each participant was first allowed to become familiar with exerting force on the load cell transducers and the resulting movements of the bar. The setup allowed the participants to produce an isometric force with their index fingers on the sensors whilst their hands rested comfortably in their laps. Following this brief practice period they received written and verbal instructions. Participants completed eleven blocks of ten repetition trials, twice, amounting to a total of 220 trials per experiment. Each trial block consisted of a possible combination of action (single or joint), hands (two or four) and dexterity (left (L) or right (R). This implied that the actors performed the action either alone with one hand (L or R) or two hands (LR) or jointly with either two (LL, LR, RL and RR) or four hands amounting to 4+2+4+1 = 11 blocks.

The eleven blocks were presented randomly. In the task conditions in which a lifting force was applied to only one end of the bar (one-handed single actions and two-handed joint actions with mixed dexterity), only the vertical position of the bar needed to be controlled. In these conditions the rotation of the bar was fixed (to horizontal). Before each trial block, both participants were presented with graphic images of left/right hands on their displays to inform the participants with which combination of hands the lifting task was to be performed. Each trial started with a constant foreperiod of 1500 ms in which the bar changed from the color red to the color orange and finally to the color black (go-signal) that indicated the start of a 6-sec recording period. As soon as the visual go-signal was presented the participants were expected to move the bar towards a target position (Figure 1 bottom panel) and retain the position of the bar between the target's upper and lower boundaries for a 2-sec period. The bar's color changed to green if the performance was successful; otherwise it remained black. At each trial completion, the final position of the bar remained visible for three seconds to allow for knowledge of results.

Data Analysis

Before the analysis, nine trials were excluded due to corrupted data. Furthermore, as we focused our study on comparable task constraints between individuals and dyads we excluded the unimanual individual condition from further analysis because it did not require the actors to balance the bar. The force-time data (1500 Hz) and resampled position-time data (75 Hz) were filtered with a second-order Butterworth, zero phase lag, low-pass filter with a cut-off frequency of 12 Hz. For each trial the filtered trajectory of the bar displacements (in pixels) and bar-orientation (in degrees) were derived.

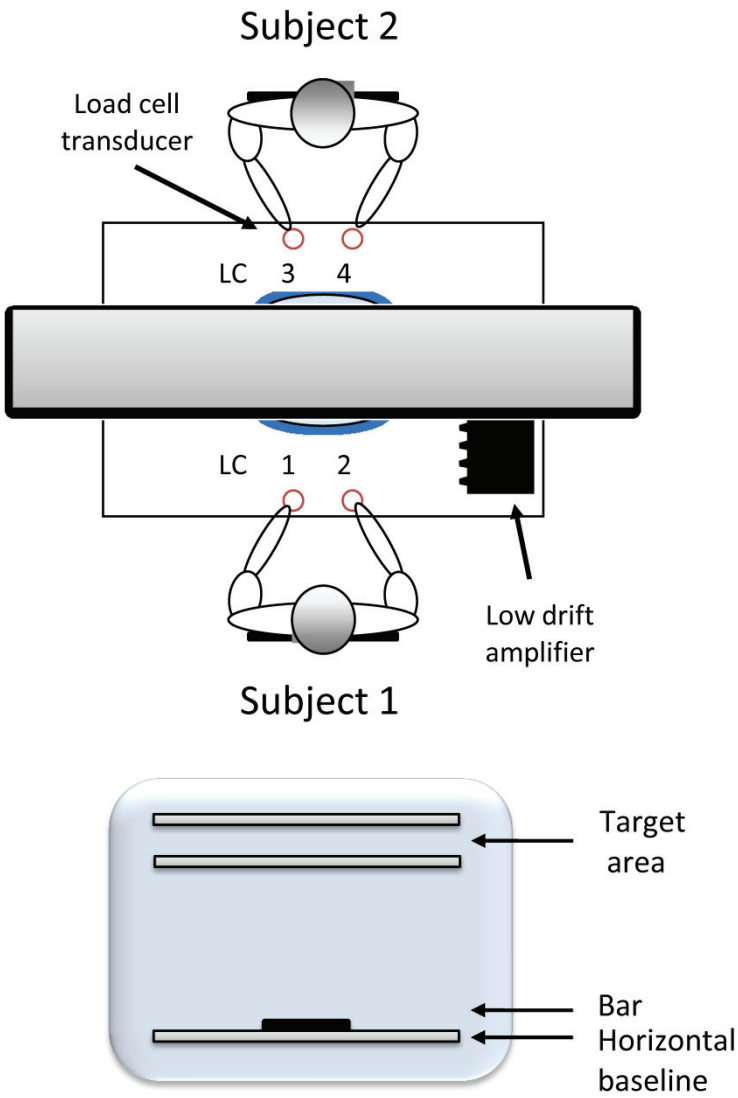

Figure 1.
The top panel shows a top view of the experimental set up. Actors (subject 1 and 2) are sitting at opposing ends of the setup, vis-à-vis, at freestanding tables that are separated by a solid freestanding screen. A monitor is placed at eye-level on the table squarely in front of each subject. The actors can apply pressure with their left (LC 1 & 4) and right index finger (LC 2 & 3) on load cell transducers that are mounted upside-down on the edge of the table and connected to a low drift instrumentation amplifier. Simultaneous pressure on a combination of LC 1 & 3 or LC 2 & 4 produced redundant force-output. The bottom panel depicts a computer display showing a black colored rectangular object (bar) resting on the horizontal baseline. Subjects were required to lift the bar between the horizontal demarcation lines (target area).

The data analyses focused on overall performance success rate, on variables that were visible to both actors in task space and variables that were only perceivable to each actor individually defined in force space.

Performance

Success rate was the percentage of trials that the participants completed successfully i.e., if the bar was held in the target area for 2000 ms.

Task Space

Four phases were identified for each trial, viz. latency, lift, stabilization and hold phase (see also Figure 2). The latency phase was the time delay between the visual go-signal (for t = 0) and the averaged time indices of the onset of sampled force production of the hands involved in the relevant task condition and was determined by means of a computer-search procedure.[6] The lift phase was defined as the time between the end of the latency phase and the first time at which both bar-ends were displaced above the lower limit boundary of the target (234 pixels). The stabilization phase was defined as the time between the lift phase and the time that the bar was contained for 2000 ms in the target area (hold phase). The stabilization phase following the lifting of the bar was identified to exclude instabilities following the lift.

The difference in absolute time (ms) of the movement onset between the left and right end of the bar was calculated (to capture the degree of synchronization in movement initiation) and the variability of bar-orientation as amount of rotation (in degrees) that the bar deviated from the horizontal orientation (0 degrees) was calculated from the discrepancy between the resampled position-time data of the left and right end of the bar. Negative values indicated a deviation in a clockwise direction and positive values indicated a deviation in a counterclockwise direction. Bar orientation was a measure of unbalanced force generation acting on the left and right bar-end. Because the force output was directly coupled to the position on the computer screen, one Newton of force difference scaled as ~5.74 degrees tilt angle. Cross-correlation functions of the bar-end displacement functions during the lift, stabilization and hold phases were used to establish the relationship between the left

[6] Criterion (search algorithm) for latency phase.
Starting at t = 0
Find for n = 20 successive samples (13.33 ms) of sampled force production (at 1500 Hz) of which:
1. Force production < 10% Maximum force production
2. Time < End of experiment
Xm = Mean force production of samples i, i+1..i+n-1
Xsd = SD force production of samples i, i+1..i+n-1
Latency = Time delay between the visual go-signal (for t = 0) and averaged time indices of first samples at which force production > Xm + 3*Xsd

and right end of the bar displacements. Time-lags were detected by an automatic search procedure for the local minima and maxima of the cross-correlation function of positional changes between the left and right side of the bar during the subsequent trial phases. We calculated the time between the extremes (minima or maxima) that occurred within each trial phase and calculated the mean cycle time (ms) per phase. We took that cycle time characterized the repetitive tuning of positional changes of the bar-ends within each trial phase. The means (Mφ) and standard deviations (STDφ) of the continuous relative-phase signals of the position-change function were calculated by using Batchelet's (1981) procedure involving circular statistics (see Meulenbroek et al., 1998) for the lift and hold phases to determine the phase difference and the stability of the phase relationships of the resulting positional changes of the bar-ends. The ten repetitions were collapsed into three grouped repetitions (GR) for which GR1 consisted of repetition 1 to 3; GR2 contained repetitions 4 to 6 and the remaining four repetitions (7 to 10) were allocated to GR3. Furthermore, the bar-orientation function was subsequently subjected to time-series analysis during the lift and hold phases by means of autocorrelation functions to reveal any systematic fluctuations in time. Time-lags were detected by a semi-automatic search procedure for relevant first local minima or the first zero-crossing if the first local minimum was unavailable. The time lags were doubled to estimate cycle durations and converted to Hz. The temporal features of these autocorrelation functions were taken to reflect the dynamics of corrective movements.

Force Space

In force space, kinetic parameters were derived from the load cells to capture the degree of coordination between forces generated by individuals performing with two hands and by dyads performing the task with two and all four hands. The amount of force that was applied to each load cell was recorded and converted to Newtons. Between-subject force productions were further determined for redundant and non-redundant force relationships (see caption of Figure 1 top-panel). Between-subject *redundant* force productions described relationships between supernumerary force productions whereby two hands jointly resulted in a displacement of either the left or right end of the bar. By contrast, between-subject *non-redundant* force production described relationships between force productions that were not supernumerary whereby two hands resulted in a combined left/right or right/left displacement of the bar and thus acted complementary by nature of the task constraints. Cross-correlations during the lift, stabilization and hold phases were used to establish the within-subject and between-subject (redundant and non-redundant joint actions) force-time relationship between force productions of the hands.

Statistical Evaluation

Sign tests were used to evaluate the degree to which observed differences between successful and unsuccessful performance was statistically significant across solos and dyads. We used paired samples t-tests to evaluate the differences between the 1-actor/2-hands and 2-actors/2-hands conditions. We also used paired samples t-tests in the 2-actor/4-hands condition to statistically evaluate the cross-correlations and the mean and standard deviations of the relative phase functions of positional changes between grouped repetitions during the lift and hold phases. The critical value for Pearson's r was set at the .05 level. Furthermore, for statistical evaluation of the correlation functions, the Pearson's r's were transformed to the normally distributed variable z' by means of the Fisher's z' transform. Bonferroni corrections were applied whenever multiple tests were conducted.

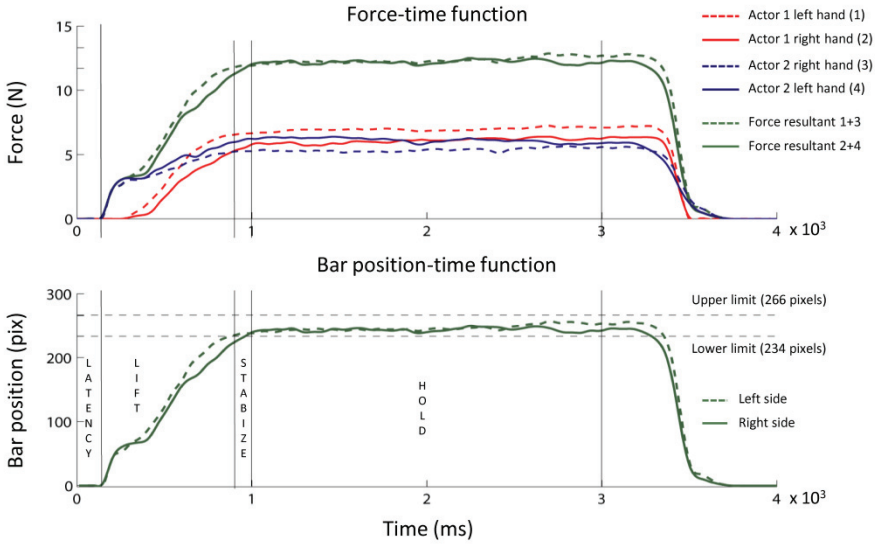

Figure 2.
Plots of the temporal patterns of the forces (top panel) bar position changes (bottom panel) in a trial that was performed successfully. Different trial phases of the task (Latency, Lift, Stabilize and Hold) are depicted by the vertical demarcation lines. The top panel shows the force data that were extracted from a condition in which subject-pairs (dyads) performed the trial with four hands for the tenth consecutive time, viz. left (dashed red plot) and right (solid red plot) hand actor 1 and right (dashed blue plot) and left (solid blue plot) hand actor 2 and the force resultants (dashed and solid green plots). The bottom panel shows the resulting positional changes of the left (dashed green plot) and right (solid green plot) bar-ends. The dashed horizontal demarcation lines (upper and lower limits) enclose the target area.

Results

Figure 2 shows plots of the force-time functions and their resultants (top panel) and the position-time functions of the left and right bar-end (bottom panel) observed in a trial that was performed successfully.

These data are typical for the task execution of the individual participants as well as the dyads. The top panel shows the data that were extracted from a condition in which two actors performed the trial with both hands. Actor 2 led the way in force initialization (~150 ms) and actor 1 followed (~290 ms). After positioning the bar into the target area, both actors maintained forces at approximately the same level with both hands whilst forces between supernumerary contributions changed reciprocally. This process occurred gradually during the full hold phase until the performance criterion of the hold phase (i.e. maintaining the bar at the correct position for 2 s) was reached.

The forces shown in the top panel of this figure resulted in positional changes of the bar-ends as shown in the bottom panel. The bar started moving after a latency of about 150 ms after the go-signal was given. Once both bar-ends were put into motion, the bar was lifted rapidly until both bar-ends approached the target area. Duration of the lifting phase was approximately 900 ms. After stabilizing the bar into the target area (~100 ms) the participants held the bar within the target area for the predefined 2-s period (holding phase).

Success Rate

Task performance was successful in 89% of the trials. For all dyads (N=10) successful trials outnumbered unsuccessful ones (sign test, N=10, $p<.05$). On average, success rates were for the 1-actor/2-hands, 2-actors/2-hands, and 2-actors/4-hands conditions 87.75%, 86.31%, 93.47%, respectively.

For the following results we used the data set containing trials that were performed successfully.

Single and Non-redundant Joint action

Targeted comparisons between the 1-actor/2-hands and 2-actors/2-hands conditions (Table 1) showed that reaction times for these two conditions were statistically indistinguishable (Duration; $t(9) = 0.561$, ns) whilst synchronization was significantly stronger for individuals than for dyads performing with two hands (ΔRT; $t(9) = 9.023$, $p<.01$). Individuals, as opposed to dyads, were able to combine a fast lift (Duration; $t(9) = 5.115$, $p<.01$) with low variability in bar orientation (SDO; $t(9) = 6.710$, $p<.01$) during the lifting phase. Table 1 shows that enhanced lifting performance by individuals is also reflected in cross-correlations and continuous relative phase analyses, i.e., relationships between the left and right bar-

ends were stronger positive (Pearson; t (9) = 11.434, p<.01), phase differences were smaller (Mφ; t (9) = 2.963, p<.05) and relatively more stable (SDφ; t (9) = 5.235, p<.01) in individuals than in dyads.

Whilst targeted comparisons showed that cycle time for positional change of the bar-ends for these two conditions were statistically indistinguishable (Cycle Time; t (9) = 1.322, ns), the basic frequency of corrective movements of the bar position during the lifting phase was significantly higher for individuals than for dyads performing with two hands (F0; t (9) = 3.197, p<.05).

Table 1.
Means and standard deviations of trial-phase duration (Duration) and synchronization of movement initiation (ΔRT) during the latency phase as a function of Actor(s)/Hands (1-actor/2-hands, 2-actors/2-hands and 2-actors/4-hands). Means and standard deviations of deviation of bar-orientation (SD BO), Cycle Time and average cross-correlations (Pearson) for Trial phase (lifting, stabilization and holding) as a function of Actor(s)/Hands. Means and standard deviations of mean relative phase (Mφ), SD relative phase (SDφ) and natural oscillation frequency (F0) for Trial phase (lifting and holding) as a function of Actor(s)/Hands.

Trial phase	Actor(s)/Hands	Duration (ms)	RT (ms)	SDO (deg)	Cycle Time (ms)	Pearson	Mϕ (deg)	SDϕ (deg)	F0 (Hz)
Latency	1-actor/2-hands	276 [62]	33 [13]						
	2-actors/2-hands	280 [69]	85 [21]						
	2-actors/4-hands	245 [83]	32 [16]						
Lifting	1-actor/2-hands	1219 [390]		3.94 [0.95]	233 [25]	0.99	7.25 [1.18]	54.15 [11.03]	1.46 [0.21]
	2-actors/2-hands	1485 [409]		11.21 [3.84]	247 [41]	0.94	7.46 [0.99]	67.91 [14.05]	1.16 [0.28]
	2-actors/4-hands	1111 [453]		2.51 [2.37]	233 [37]	0.99	6.42 [1.56]	53.94 [12.91]	1.35 [0.25]
Stabilizing	1-actor/2-hands	601 [366]		2.14 [0.83]	182 [19]	0.26			
	2-actors/2-hands	886 [291]		3.68 [1.86]	175 [22]	0.08			
	2-actors/4-hands	557 [333]		2.10 [1.85]		0.23			
Holding	1-actor/2-hands			1.18 [0.12]	145 [11]	0.3	7.46 [1.24]	59.35 [5.96]	1.13 [0.12]
	2-actors/2-hands			1.39 [0.18]	147 [10]	-0.01	11.4 [2.11]	74.60 [12.00]	1.19 [0.13]
	2-actors/4-hands			0.99 [0.78]	150 [10]	0.28	8.78 [1.67]	57.35 [8.17]	1.20 [0.24]

Also during the stabilization phase, individuals performed better than dyads (Table 1). Individuals were able to stabilize the bar faster (Duration; t (9) = 4.372, p<.01) and showed smaller bar-orientation variability (SDO; t (9) = 7.324, p<.01) than dyads. Table 1 also shows that the correlations between the left and right bar-ends were uncoupled in both individuals (Pearson; r(40) = +0.26, ns) and dyads (Pearson; r(40) = +0.08, ns) whilst cycle time between the targeted comparisons were statistically indistinguishable for these two conditions (Cycle Time; t (9) = 1.240, ns). During the holding phase bar variability was slightly, but significantly, lower in individual performance than in performance by dyads (SDO; t (9) = 7.324, p<.01).

Furthermore relationships between the left and right bar-ends were stronger positive in single than in joint action (Pearson; t (9) = 11.195, p<.01). Phase differences between bar-ends were smaller (Mφ; t (9) = 8.075, p<.01) and relatively more stable (SDφ; t (9) = 5.195, p<.01) for individuals than for dyads whilst cycle time for positional change of the bar-ends (Cycle Time; t (9) = 1.571, ns) and the basic frequency of corrective movements of the bar position during the holding phase (F0; t (9) = 1.235, ns) were statistically indistinguishable for these two conditions.

Table 2.
Means (Mφ) and standard deviations (STDφ) of the continuous relative-phase signals of the position-change function for grouped repetitions (GR1, GR2 and GR3) during Trial phases (Lifting and Holding) as a function of Actor(s)/Hands (1-actor/2-hands, 2-actors/2-hands and 2-actors/4-hands).

Trial phase	Actor(s)/Hands		Mϕ (deg)	SDϕ (deg)
Lifting	1-actor/2-hands	GR1	9.45 [3.03]	60.23 [11.73]
		GR2	8.41 [1.96]	50.60 [10.90] *
		GR3	8.20 [2.02]	51.95 [13.45]
	2-actors/2-hands	GR1	15.02 [5.34]	75.63 [12.97]
		GR2	10.15 [5.02] **	69.40 [15.96]
		GR3	9.93 [2.75]	61.44 [16.01] **
	2-actors/4-hands	GR1	7.14 [2.90]	61.81 [18.95]
		GR2	6.81 [1.49]	51.69 [13.55] **
		GR3	6.06 [2.02]	51.48 [12.10]
Holding	1-actor/2hands	GR1	7.54 [2.65]	63.26 [5.77]
		GR2	7.49 [2.26]	58.97 [9.94]
		GR3	7.82 [2.08]	57.05 [11.61]
	2-actors/2-hands	GR1	12.75 [4.41]	73.44 [14.47]
		GR2	11.49 [3.32]	74.02 [12.86]
		GR3	12.01 [2.77]	75.01 [11.45]
	2-actors/4-hands	GR1	9.92 [1.64]	62.19 [5.46]
		GR2	8.13 [2.77]	52.43 [10.98] **
		GR3	8.89 [2.14]	53.74 [12.96]

* p < 0.01, ** p < 0.05

During lifting, the mean phase differences (Mφ) for positional changes between bar-ends in individual performance (Table 2) were comparable across the three grouped repetitions whilst the stability of these phase relationships increased from GR1 to GR2 (SDφ; t (9) = 3.574, p<.01) and were statistically indistinguishable between GR2 and GR3 (SDφ; t (9) = 0.731, ns). In dyads, these phase differences decreased significantly from GR1 to GR2 (Mφ; t (9) = 2.461, p<.05) whilst GR2 and GR3 were statistically indistinguishable (Mφ; t (9) = 0.173, ns). The stability of these phase relationships increased significantly from GR2 to GR3 (SD; t (9) = 2.929, p<.05) whilst GR1 and GR2 were statistically indistinguishable (SDφ; t (9) = 1.851, ns) during lifting.

During the holding phase, phase differences for positional changes between bar-ends for individuals between GR1, GR2 and GR3 and the stability of these phase relationships GR1, GR2 and GR3 remained comparable across the grouped repetitions. Also phase differences for dyads between GR1, GR2 and GR3 and the stability of the phase relationships GR1, GR2 and GR3 remained comparable across the grouped repetitions.

In sum, both individuals and dyads were equally fast in preparing and initiating the movement in the targeted conditions. However individuals were faster than dyads in lifting and stabilizing the bar, exerting faster movement corrections during the lifting phase. Overall relationships between both bar-ends were stronger positive, with smaller phase differences and were performed relatively more stable by individuals than by dyads. Furthermore, phase relationships for positional changes between bar-ends during lifting showed systematic changes over trial repetitions.

Redundant Joint Action

Overall performance by dyads executing the task with four hands was assessed (see Table 1) with respect to movement initiation, synchronization of movement initiation, lifting time and stabilization time, balancing of both bar-ends during the lifting, stabilization and holding phases.

Correlations between bar-ends were, on average, strong positive (Pearson; r(70) = +0.99, p<.01) during the lift, uncoupled during stabilization (r(40) = +0.23, ns) and weakly positive during holding (Pearson; r(70) = +0.28, p<.01). Phase differences of positional changes between bar-ends were relatively small during lifting and relatively larger during holding. These relationships were relatively more stable during the lifting phase than during the holding phase. Cycle time of the position-change function of the bar was higher for lifting than for holding the bar whereas the basic frequency of the corrective movements of the bar were in the same order for the lifting and holding phase .

In the lifting phase (see Table 2), the Mφ for positional changes between bar-ends was comparable across the grouped repetitions whilst the stability of these phase

relationships increased from GR1 to GR2 (SDφ; t (9) = 3.018, p<.05) and were statistically indistinguishable between GR2 and GR3 (SDφ; t (9) = 0.057, ns).

During the holding phase, phase differences for positional changes between bar-ends remained comparable across the grouped repetitions. The stability of these phase relationships showed an increase from GR1 to GR2 (SDφ; t (9) = 2.512, p<.05), whilst the SDφ between GR2 and GR3 were statistically indistinguishable (SDφ; t (9) = 0. 297, ns).

These results show that dyads in redundant joint action combined a relative fast task execution with a low variability in bar orientation. They displayed a systematic increase in stable phase relationships across grouped repetitions in the lifting and holding phases. Overall, relationships between bar-ends were stronger positive, displayed smaller phase differences and were relatively more stable during lifting than holding the bar. Furthermore, low-frequency action-monitoring feedback loops were in the order of 1 Hz during the lift and hold phases.

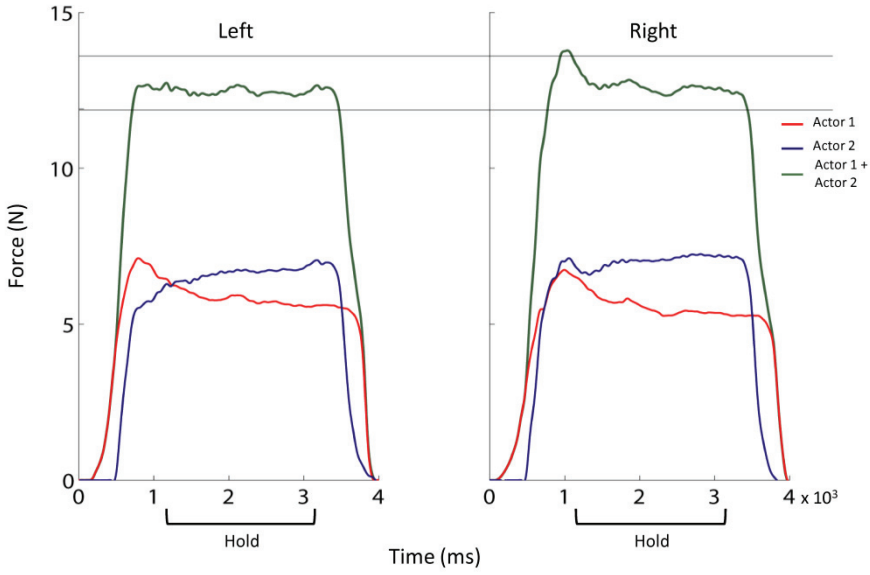

Figure 3.
Example of a single-trial plot of the temporal patterns of the forces and force resultants for dyads performing the trial successfully with four hands for the seventh consecutive time. Red plots indicate force contributions by actor 1 and blue plots indicate force contributions by actor 2 whilst green plots indicate force resultants acting on the left and right bar sides.

Figure 3 shows force relationships of a single trial that reflect the typical performance of dyads performing with four hands. During the holding phase, forces of both hands of actor 1 decreased simultaneously whilst, at the same time, forces of both hands of actor 2 increased synchronously resulting in reciprocally gradually changing supernumerary force contributions. The figure displays strong negative correlations between supernumerary forces between actors viz. ($r(70) = -0.90$, $p<.01$) in the left panel and ($r(70) = -0.80$, $p<.01$) in the right panel. Furthermore correlations between both hands of actor 1 ($r(70) = +0.92$, $p<.01$) and actor 2 ($r(70) = +0.86$, $p<.01$) were strong positive whilst correlations between the force resultants were weakly positive ($r(70) = +0.39$, $p<.01$).

This single-trial observation is substantiated by the overall results of within-subject and between-subject redundant and non-redundant force contributions of dyads performing the experimental task with four hands (Figure 4).

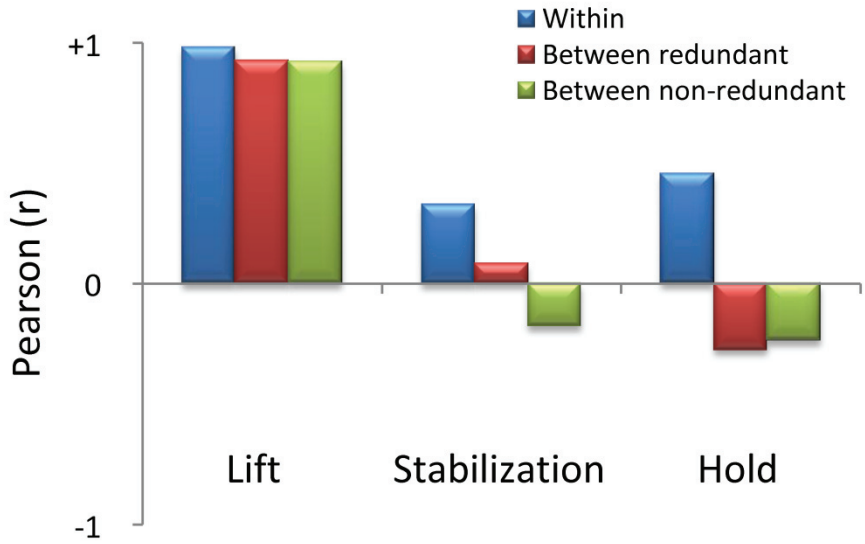

Figure 4.
Within-subject (red), between-subject redundant (blue) and between-subject non-redundant (green) bar plots represent the means of the cross-correlations function (Pearson r) between force producing hands of dyads in redundant joint action during the lifting, stabilization and lifting phases.

Figure 4 shows the cross-correlations between the contributing forces for dyads in redundant joint action during the lifting, stabilization and holding phases. During the lift, within-subject correlations in the 2-actors/4-hands condition ($r(70) = +0.98$,

$p<.01$) were higher than between-subject redundant ($r(70) = +0.93$, $p<.01$; $t(9) = 7.225$, $p<.01$) and non-redundant ($r(70) = +0.92$, $p<.01$; $t(9) = 6.553$, $p<.01$) correlations, whilst between-subject redundant and non-redundant correlations were statistically indistinguishable ($t(9) = 1.653$, ns). On average, force relationships for dyads performing with four hands during the stabilization phase were weakly positive ($r(40) = +0.33$, $p<.05$) for the within-subject correlations, whilst between-subject redundant ($r(40) = +0.08$, ns) and between-subject non-redundant ($r(40) = -0.18$, ns) correlations were absent. During the holding phase, correlations for the within-subject forces were, on average, weakly positive ($r(70) = +0.46$, $p<.01$) and significantly different than correlations for the weakly negative between-subject redundant force contributions ($r(70) = -0.27$, $p<.05$; $t(9) = 4.447$, $p<.01$) and for the weakly negative between-subject non-redundant forces ($r(70) = -0.24$, $p<.05$; $t(9) = 3.979$, $p<.01$). Correlations for between-subject redundant forces and non-redundant forces were statistically indistinguishable ($t(9) = 1.116$, ns).

In sum, within-subject relationships between force contributions of dyads performing with four hands ranged from high positive to weakly positive whilst between-subject relationships ranged from high positive during the lifting phase to weakly negative during the holding phase.

Discussion

In this study we investigated redundancy control when two people performed an isometric force-production, virtual bar-lifting task. Participants executed the isometric lifting task alone bimanually and together either with two or with all four hands and could not see each other and were not allowed to verbally communicate. Not only did individuals and dyads have to transport the bar into a target area and *hold* it there for a two-second period, but unbalanced force generation resulted in a tilt (rotation) of the bar in the frontal plane. Our aim was to assess the features of the individual and group contributions to the action and to capture the temporal characteristics of their coordinated attempt to adjust both the height and rotation of the bar in their task performance. In performing the isometric lifting task with four hands, the system was overspecified and task-specific structural units (synergies) between the force-producing hands were presumed to be created. One may hypothesize that at the level of movement planning these structural units simplify the control problem. The present findings provide, in our view, an indication that lacking a shared neural substrate and diminished sensory information does not necessarily present individuals with an unbridgeable gap to work together. Under such conditions dyads can create task-specific structural units, even though group members will execute tasks that they perform together slower than individuals do and may perform poorly on synchronizing their actions.

Single and Non-redundant Joint action

Individuals were, as expected, better in synchronizing both bar-ends after movement initiation than dyads, and outperformed dyads in lifting and stabilizing the bar, exerting faster movement corrections during the lifting phase and individuals also displayed more skill in controlling the tilt of the bar throughout all phases of the trial (Table 1). These observations are in line with results in previous studies (Burstedt et al., 1997; Schmidt et al., 1998; Knoblich et al., 2003) that have shown performance to be impeded in joint action if the task at hand requires dyads to time their actions together.

The higher performance by individuals is reflected by cross-correlations analysis of position-time functions of the bar and continuous relative phase analysis of positional changes of both bar-ends that were applied to uncover the dynamics of the coordination underlying the control of bar movements (see Table 1 and Table 2). Individuals, as opposed to dyads, realized stronger phase coupling, maintained relatively more stable phase relationships between both bar-ends and upheld stronger positive correlations between bar-ends during the lifting and holding phases. On the other hands, dyads only displayed strong positive correlations during the lifting phase. However, the strong positive correlations during the lift hardly provide strong evidence of synchronized joint action. For example, sprinters participating in the 100 m finals of a race event will all be out of the starting blocks in roughly the same time after the starting signal but obviously have no interest to intentionally coordinate their actions amongst each other during the race. We therefore take these results to reflect performance that is dictated by the synchronized "go" signal whilst aiming for a common goal (see also Figure 4; subsection Redundant Joint Action).

A possible explanation for enhanced performance in individuals can be found by presupposing that they received both fast haptic feedback loops from tactile afferents of the fingertips and relative slow online visual feedback of the bar displacements on the computer screen whilst dyads could only rely on relative slow online visual feedback of their partners' actions to perceive the consequences of their actions. However, cycle time, as a measure of repetitive tuning of positional changes of the bar-ends, was in the same order within each trial phase for both individuals and dyads (see Table 1) indicating that individuals also mainly relied on visual-motor feedback loops to monitor their actions. Because the two hands of the individual are anatomically linked they were able realize a proactive coordination regime and execute corrective movements more often during the lifting phase than dyads.

Even though dyads do not share a common neural substrate, they were as successful as individuals in performing the experimental task. Moreover, dyads also displayed adaptive behavior over trial repetitions during the lifting phase, be it that dyads were

slower in adapting to the requirements of the task dynamics than individuals (see Table 2). Whilst individuals quickly learned to produce more stable interactions between both bar-ends over trial repetitions, dyads responded first by reducing phase differences between contributing hands and at a later stage increased the stability of these interactions.

Surprisingly, both individuals and dyads in the two-handed conditions were equally fast in preparing and initiating the movement. "Surprisingly", because performance by dyads in the two-handed condition could, technically speaking, be viewed as a one-handed performance by two separate actors and unilateral movements have been shown to take shorter to initiate than simultaneous bilateral single-actions carried out by two hands (Kelso et al., 1979; Ohtsuki, 1994). Swinnen and Wenderoth (2004) have argued that within the information-processing perspective, dual-task performance by one brain is faced with structural interference. This concept of neural crosstalk presupposes that information leakage may occur at different levels of the central nervous system (cortical to spinal), both during bimanual motor programming and execution. Consequently, during motor programming and initializing of the movement, dyads in the two-handed condition, must have taken each others preparation for the task into account. We find support for our observation in a number of studies concerning discrete tasks, showing, that an efficient means to predict others' actions that is not necessarily based on action observation but knowing what another's task is (Sebanz & Frith, 2004; Sebanz, Knoblich & Prinz, 2005). By forming shared task representations, it is possible to predict actions based on certain events in the environment, independent of action observation (Sebanz, Bekkering & Knoblich, 2006).

Redundant Joint Action

An expected key finding in this study is that correlations between supernumerary force contributions by dyads performing the task with four hands, during the holding phase, were found to be negative (Figure 4). This means that interacting partners not only responded to observed changes but also incorporated the timing of the actions of the partner in their own action planning. This feature of joint action is remarkable if we take into consideration that the contributions to the lifting task by one partner were not directly observable for the other i.e., dyads acted on relative slow online visual feedback of the composite adjustments that they jointly brought about.

Of course, dyads would not necessarily have to remain ignorant of their partner's contribution to the task. For example, by first giving an arbitrary battery of force outputs for system identification purposes and then by generating error measures from the internal predictions of their own movements (Wolpert & Ghahramani, 2000) and the observed joint-movements on screen, the error measures would allow them to assess their partner's contribution to the task. It is obvious that the type of

coordination that evolves from this course of action is reactive in nature (i.e., successive actions are produced on the basis of inferring the composite feedback) and therefore may not seem to provide a means of modeling synchronized action coordination in redundant joint action.

Both intentional synchronization of movements (Schmidt et al, 1994) and unintentional synchronization of movements (Schmidt et al., 1990; Schmidt & O'Brien, 1997) have been observed for the swinging of hand-held pendulums by pairs of participants when they can see each other's movements and modeled by the Haken, Kelso and Bunz (1985) model and its modifications (Kelso & Jeka, 1992; Fuchs & Kelso, 1994). However, it is not clear how the Haken et al. (1985) model is able to deal with the absence of direct visual feedback of the partners' contributions to the task (see also Rosenbaum et al., 2006).

Negative correlations during the holding phase could also indicate that the task at hand is to be viewed as a tracking task. Because now that the bar is in the proper place with the proper orientation, each person is visually "tracking" the other, in other words we have compensatory tracking and of course there will be a negative correlation between the error and the correction to it, which is the definition of negative feedback.

Because the output to the lifting task was composed of both actors' actions, dyads had no direct feedback of their partner's contributions to the task. This means that dyads in redundant conditions can only compensate for the error they mutually bring about, thereby leaving out the possibility that each person "tracks" the other and thereby the presumption that the task during the holding phase can be viewed as a compensatory tracking task.

On the other hand, research has also shown that actors can learn to make accurate force-related predictions (Dizio & Lackner, 1995; Shadmehr & Mussa-Ivaldi, 1994) as well as adaptive anticipatory changes to altered visual feedback, as in prism adaptation (Redding & Wallace, 1997) by forming an internal model of the joint-dynamics of the action of which they are part of (cf. Atkeson, 1989; Jordan, 1994). We assume that adaptive behavior would therefore enable dyads to generate forces that anticipate rather than merely react to the actions of their counterpart.

Our results show (Table 2) that dyads performing redundant joint action quickly increased stable phase relationships between both bar-ends over trial repetitions in both the lifting and holding phases. This implies that dyads were quite capable of displaying adaptive behavior by the contributing forces in controlling both dimensions of the bar in the course of trial repetitions.

The present results did not reveal a joint-action coordination strategy of perfect degree-of-freedom allocation across the participants, i.e., one actor taking care of the height of the bar and the other controlling its rotation. Dyads performing the task

with four hands could have developed a cooperative strategy such that one member contributed more to the height and the other to constraining the rotation of the bar. However, Figure 4 shows that those dyads created three synergies that operated in synchrony during the holding phase. Each of the actors created a separate synergy by coupling positional changes of bar-ends to control the bar-orientation, and at the same time, these synergies were inversely coupled to jointly control the bar height. These findings underline our conclusion that, in the redundant joint action, both actors show a strong tendency to take their share in controlling both task dimensions in order to perform the task at hand successfully.

Typically, the generated forces increased or decreased very gradually throughout the holding phase, as can be observed in the single-trial plots shown in Figure 3. Analyses of autocorrelation functions revealed that the bar-orientation time-functions displayed an average periodicity of 1.17 Hz. We take that these regularly recurring changes in bar orientation are indicative of low-frequency feedback loops that subserve action-monitoring functions whilst holding the bar in place. Studies in which the intermittency of visual feedback was manipulated while people tried to maintain a steady force level have shown that action-monitoring functions in individuals also seem to be governed by low-frequency feedback loops (Slifkin, Vaillancourt & Newell, 2000; Sosnoff & Newell, 2005). We take that the gradual changes in bar-orientation in the present study are due to positional drift as an effect of diminished visual feedback. Research into hand-position matching have shown that without vision, the accuracy with which finger locations are reported declines over repeated matches such that perception of limb position appears to drift (Paillard & Brouchon, 1968; Wann & Ibrahim ,1993; Wolpert, Goodbody & Husain, 1998). Due to the gradual nature of the changes in bar-orientation during the holding phase in this experiment, actors are provided with ample time to effectively plan their action over time and counterbalance for the positional drift by low-frequency modulated forces to keep their performance tuned to task demands.

In general, our results show that the coupling of effectors does not depend on whether their neural control centers are anatomically linked and confirms earlier suggestions that such coupling may be informationally and not just anatomically based. Furthermore, the results indicate the presence of homogeneously attuned forces, synchronized by the “go” signal to make a common cause in lifting, that the forces were reactive in nature during the stabilization phase to serve as an upbeat for holding the bar in place where inverse force relationships between supernumerary force contributions indicate that dyads were capable of resolving redundancy by administering force-sharing synergies that, in our view, certifies the signature of synchronized joint-action in our experimental task.

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Chapter 5

Interpersonal Movement Coordination in Amplitude-Frequency Control on a Rocking Board

Abstract

In this study we investigate how two people coordinate their movements while standing on a rocking board, which they have to rock from side to side with varying amplitudes and frequencies. We focus on the relative amount of predictive motor control in conditions in which the two participants stand face-to-face (i.e. while seeing each other) and back-to-back (i.e. without seeing each other). Twelve subject pairs (dyads) performed side-to-side rocking movements on a board in nine conditions covering three amplitudes (8, 18 and 28 degrees) and three frequencies (0.4, 0.6 and 0.8 Hz). The instructed and realized amplitude-frequency combinations were presented real-time on computer displays in the form of rotating bars. By means of a 3D-motion tracking system (Optotrak 3020, 75 Hz) we measured the displacements of 28 infrared light emitting diodes that were attached to the balancing board, and to the head, ankles, knees, hips, and shoulders of each actor. From these data, we derived the joint rotations and the continuous relative phase of relevant joint-angle pairs. Furthermore, we examined whether corrections to amplitude and frequency errors were negatively correlated (reflecting exploitation of biomechanics) or positively correlated (requiring deliberate control). We expect to identify different intrapersonal synergies and interpersonal perception-action couplings depending on whether participants faced each other or stood back-to-back. We also expect that when people are simultaneously confronted with spatial and temporal constraints in this repetitive motor task, they will either exploit the biomechanical amplitude-frequency relationships or adopt a cognitive strategy to control frequency and amplitude. Our method comprises a new way of inferring deliberate, low-dimensional control of joint action in a high-dimensional, rocking board task.

Introduction

Most studies of interpersonal movement coordination have, to date, focused on the tacit entrainment of rhythmic motion patterns in tasks that lack any shared action goal (see e.g. Schmidt & O'Brien, 1997; Richardson et al., 2006). In the present study we investigated how subject pairs coordinate their movements when deliberately trying, on a rocking board, to track a visually presented motion pattern. In particular, we asked our subject pairs to jointly produce rocking movements of predefined amplitude-frequency combinations. One of the questions that we addressed - and that is central to the present report - was whether we could differentiate between incidental and deliberate control of the rocking-board movements by the dyads.

In an earlier study in which we focused on amplitude and frequency control in loop writing (Chapter 3) we demonstrated that cycle-to-cycle movement-parameter changes can be categorized as either intentional or biomechanical. Our categorization relied on the inverse relationship that normally exists between amplitude and frequency in that small amplitudes are usually generated at high frequencies whereas large amplitudes tend to be generated at low frequencies (cf. Vaughan et al., 1995). If corrections of amplitude and frequency errors from one movement to the next are negatively correlated, we assume that subjects intentionally changed only one parameter while having exploited biomechanics for the change of the other parameter (cf. Vereijken et al., 1997). Inversely, if such corrections are positively correlated we infer that subjects succeeded in simultaneously, and deliberately, changing both parameters.

To verify whether our paradigm could also be applied to the presently investigated joint-action task, we decided to contrast two conditions that we expected would modulate the extent to which dyads could exert deliberate control over their task performance. In one condition the subjects faced each other and they thus were continuously given both haptic and visual feedback of their and their co-actor's movement consequences. In the other condition, the two subjects were asked to perform the task back-to-back thus preventing them from seeing each other. In the latter condition, the consequences of the co-actor's performance could only be picked up haptically. Given the key role which the visual modality is supposed to play in interpersonal movement coordination (Schmidt & O'Brien, 1997; Richardson et al., 2006), the frequency of intentional motion parameter changes was expected to be lower in the back-to-back than in the vis-à-vis condition.

Method

Participants

Twenty-eight psychology students from the University of Nijmegen participated in our study. Their age ranged between 22 and 27 years. All participants had normal or corrected-to-normal vision and none had motor problems. All participants gave their informed consent and were rewarded for their participation with either course credits or payment of 12 Euros. Experimental procedures followed the APA guidelines for the ethical treatment of human participants.

Figure 1. Experimental setup

Task and Procedure

The participants were randomly paired and given written instructions before the experimental session began. The subject-pairs (dyads) stood on a 200x60 cm wooden rocking board with the base pad covered in non-slip surface as customary used in physiotherapy for proprioceptive training (see Figure 1). The board with a 30 degree tilt could only rock in one dimension (x-dimension). Each participant performed side-to-side rocking movements in nine conditions covering three amplitudes (8, 18 and 28 degrees) and three frequencies (0.4, 0.6 and 0.8 Hz).

Furthermore the task was executed by each participant individually or as a dyad. When together, they were placed in two different stances viz.: vis-à-vis (seeing each other) and back-to-back (not seeing each other). The instructed and realized amplitude-frequency combinations were presented real-time on computer displays in the form of rotating bars. Participants were asked to track the target movements by jointly rocking the board sideways while receiving continuous visual feedback of its rotations. They were not allowed to communicate verbally with each other. Before the experiment started, participants were allowed to practice the task a few times to get comfortable with controlling the movements of the rocking board.

The 30-s trial started when the target bar began to tilt and ended when the target bar ceased to rock. Each experimental session consisted of four blocks of 27 trials leading to a total of 108 trials for each session. The first and fourth trial block was always a joint-action condition be it the participants facing each other or standing back-to-back. In the second and third block the participants performed individually. All blocks were counterbalanced across the experiment. By structuring the sessions in this manner, participants were spared to perform more than 54 trials in succession. Each block consisted of three repetitions of the nine amplitude-frequency combinations that were presented at random.

Data acquisition

Three rigid bodies, each consisting of four infrared light emitting diodes (IREDs) fixated at a 1 × 1 × 1 × 1 cm inter-IRED distance on a flat aluminum plate were consecutively mounted on the base pad of the rocking board and strapped onto the foreheads of each participant. Next, 16 infrared light emitting diodes were attached to the ankles, knees, hips, and upper trunk (over the Coracoid process) of each actor. Translations of the IREDS and rotations of the rigid bodies were recorded at a rate of 75 Hz and with a spatial accuracy higher than 0.2 mm in the *x, y* and *z* direction by means of a 3D-motion tracking system (Optotrak 3020, Northern Digital Inc., Waterloo, Canada). At the same time, the instructed and realized angular rotations of the rocking board were sampled real-time at a rate of 38.7 Hz and recorded into a separate file. The intrapersonal coordination captured by the recording of the IREDs on the participants' bodies was not analyzed for the purpose of the present paper. The results of those analyses will be reported elsewhere.

Data Analysis

The instructed and realized angular rocking movements were resampled to 75 Hz and filtered with a second-order, dual-pass Butterworth filter. The high-pass frequency was 0.5 Hz for all signals and the low-pass cut-off frequency of the filter was set to twice the pacing frequency of the condition in which the signal was recorded. This ensured that an automatic peak-peak detection algorithm could be

applied reliably. On the basis of this algorithm, successive cycles were extracted of which the first and last cycle of the trial were not included in the analysis.

For each obtained rocking cycle, the realized amplitude A, expressed in mm, in the x-dimension was calculated. A similar procedure was applied to arrive at a local cycle frequency, *F*, expressed in Hz. Next, the parameters A and *F* were used to calculate the local spatial error, A_{err}, expressed as a percentage of the instructed amplitude, where positive values reflected amplitude overshoots and negative amplitudes reflected amplitude undershoots. Similarly, the local frequency error, $F_{err,}$ was expressed as a percentage of the instructed frequency, where positive values reflected higher than instructed frequencies and negative values represented lower than instructed frequencies. The next step concerned quantifying the error changes from one cycle to the next. Except for the first movement cycle in each trial, we obtained for each cycle, the two parameters ΔA_{err} and $\Delta F_{err,}$ where ΔA_{err} equalled A_{err} of cycle *i* minus A_{err} of cycle *i*-1, *and* ΔF_{err} equaled F_{err} of cycle *i* minus F_{err} of cycle *i*-1.

A minimum value, *d*, set at 1% of the local instructed parameter value, was used to identify a change in parameter value. Any absolute value greater than or equal to this value qualified as a parameter-value change. We first categorized the A_{err} and F_{err} data into the eight outer (quantitative) cells of Table 2. These eight categories represented all possible combinations of overshoots and undershoots in the amplitude and frequency domain. Subsequently, each ΔA_{err} and ΔF_{err} combination, representing the error change realized from one movement to the next, was classified as a single-parameter change or as a double-parameter change or as a quasi-double parameter change.

The critical value for statistical significance was set at the .05 level. Sign tests were used to evaluate the statistical significance of observed differences between the incidences of movement-error categories and categories of parameter changes. These non-parametric tests were more conservative than Chi-square tests in this context. Repeated measures ANOVAs were applied to evaluate the continuous movement parameters.

Results

Realized amplitudes and frequencies

All dyads produced, on average, the instructed movement amplitudes and frequencies accurately (see Table 1).

The realized amplitudes decreased somewhat as the imposed frequencies increased ($F(2,26)=15.12$, $p<.01$). The reverse was not true, however. The realized frequencies

slightly increased as the imposed amplitudes increased ($F(2,26)=4.76$, $p<.05$). We will return to this deviating finding in the discussion.

Table 1.
Left-hand panel: instructed and realized mean amplitudes (standard deviations between brackets) pooled across frequency conditions. Right-hand panel: instructed and realized mean frequencies (standard deviations between brackets) pooled across amplitude conditions.

Amplitude (deg)	
Instructed	Realized
8	10.00 [1.94] **
18	18.06 [2.44] **
28	23.87 [2.83] **

Frequency (Hz)	
Instructed	Realized
0.4	0.41 [0.03] **
0.6	0.61 [0.05] **
0.8	0.80 [0.04] **

** $p < .05$

Amplitude and frequency errors

All fourteen dyads produced a total of 19,734 movement cycles that were evaluated in terms of the realized amplitude and frequency relative to the instructed amplitude and frequency. Table 2 shows the frequency distribution of performance errors categorized per cycle but collapsed over the three instructed amplitude and frequency conditions.

At the center of Table 2 the proportion of movements for which both the amplitude and frequency were on target. Note that, as expected, this number is low because of the stringent criterion we used to identify errors and error changes (i.e., 1% of each of the two goal parameters, see Method section). As expected, 12 out of 14 dyads

Table 2.
Incidence (%) of amplitude and frequency errors with the mean sizes of the errors between parentheses.

		Amplitude		
		Too Small	*No Error*	*Too Large*
Frequency	*Too High*	29.09% (F_{err} = +9%; A_{err} = -26%)	1.18% (F_{err} = +7%)	15.52% (F_{err} = +8%; A_{err} = +19%)
	No Error	11.83% (A_{err} = -15%)	0.84%	9.00% (A_{err} = +19)
	Too Low	20.86% (F_{err} = -9%; A_{err} = -24%)	0.74% (F_{err} = -6%)	10.94% (F_{err} = -8%; A_{err} = +21%)

produced more amplitude undershoots than amplitude overshoots (sign test, N=14, $p < .05$; cf. Gordon et al., 1995) whilst all 14 dyads produced more frequency overshoots than frequency undershoots (sign test, N=14, $p < .001$).

Parameter changes from one movement to the next

Table 3 shows the three types of parameter changes: *single* when either the amplitude or frequency changed from one cycle to the next, *double* when both parameters changed into the same direction, and *quasi-double* when one parameter increased and the other decreased or vice versa. Table 3 shows the incidence of the three types of parameter change as a function of the three categories of error changes (increase, increase/decrease, and decrease) expressed as a percentage of the local goal parameter. The latter factor reflects whether the parameter changes were goal-directed (increase) or not (decrease).

In general, participants obeyed the task instructions by trying to satisfy either one or both the requested amplitude and frequency constraints. From one movement to the next they succeeded in changing local movement parameters toward the goal

Table 3.
Frequency table of parameter changes (single, double, quasi-double; see text). The row factor (Error change) reflects whether the changes were goal-directed (increase) or not (decrease).

		Type of parameter change			
		Single	*Double*	*Quasi-double*	**Total**
Error change	*Increase*	5.90%	7.47%	13.30%	**26.67%**
	Increase & Decrease	4.91%	10.84%	21.29%	**37.03%**
	Decrease	7.14%	8.63%	18.06%	**33.83%**
	Total	**17.95%**	**26.95%**	**52.64%**	**97.54%**

movement parameters. Thus, all 14 dyads produced more movements that reduced either one or both parameter error(s) than movements that caused both local movement parameters to drift away from the goal parameter combination (sign test, N=14, $p < .001$).

All 14 dyads produced more quasi-double parameter changes (52.64%) than double parameter changes (26.95%; sign test, N=14, $p < .001$) or single-parameter changes (17.95%; sign test, N=14, $p < .001$) whilst 12 dyads produced more double than single parameter changes (sign test, N=14, $p < .05$).

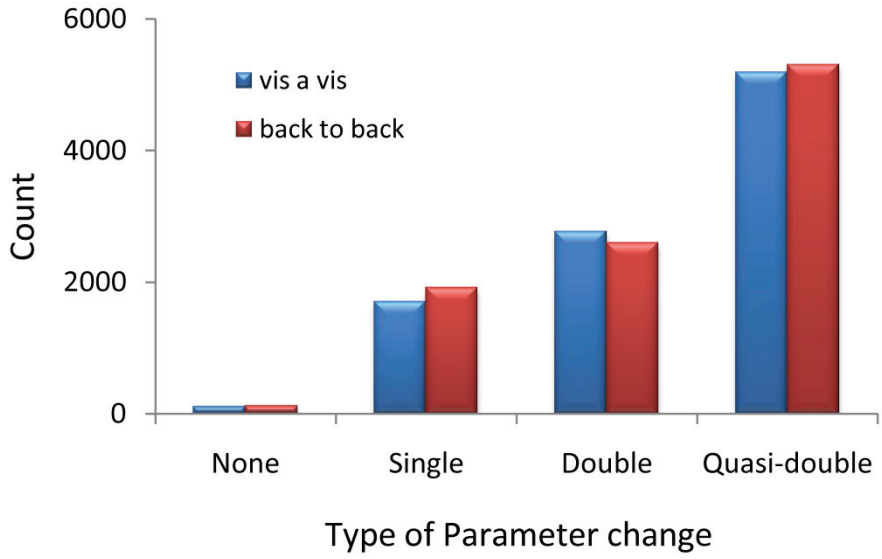

Figure 2.
Frequency of movement-parameter changes. Quasi-double parameter changes outnumber other types of cycle-to-cycle parameter adjustments, both in the condition in which the participants faced each other and in which they performed the task back-to-back.

Parameter changes independent of available modalities

Figure 2 shows the absence of any effect of the key experimental manipulation of the participants either facing each other or rocking the board back-to-back on the frequency distribution of cycle-to-cycle parameter changes. The results do not confirm our hypothesis. Even though shown in Fig. 2 by means of a cumulative count, the finding held for all dyads (sign test, $N=14$, $p < .001$).

Discussion

The present findings confirm that also in joint motor tasks in which two actors share an action goal explicitly, people manage to exploit the biomechanical relationships between movement amplitude and frequency when asked to generate specific target values of these parameters. While rhythmically moving the rocking board sideways, energy optimization most likely prompted the dyads to stick to a general strategy of amplitude undershooting. This is in line with the findings by cf. Gordon et al. (1995). The presently selected movement frequency range elicited overall frequency overshoots, probably because the preferred frequency of the rocking board, with two

adults balancing on top of it, was higher than we inferred during the piloting phase of this study. The latter might also be the cause why the realized frequencies increased with an increase of the imposed amplitudes.

As regards movement-parameter changes from one movement to the next, the present study confirms our earlier findings obtained in a study of a totally different motor task, viz., loop writing (Chapter 3). When categorizing cycle-to-cycle movement parameter changes hovering around a target parameter combination, people, also when performing a complicated motor task together, manage to exploit the biomechanical relationships of motion amplitude and frequency. In other words, they most often focus their intentional movement change on one aspect of the task and try to get the change in another task dimension for free. It is this strategy that yielded the largest incidence of quasi-double movement parameter changes from one cycle to the next.

The null results of the present study that the adopted parameter-change strategy did not vary as a function of whether the participants saw each other while performing the task or not, are, in our view, informative (cf. Harcum, 1990). They demonstrate that exploitation of biomechanics in goal-directed task performance is a prominent motor control mechanism that seems to be independent of the modalities used for monitoring the perceptual consequences of the generated motion patterns. Whether or not modality-dependent variations occurred with respect to intra- and interpersonal *joint coordination*, where joint now refers to the linkage between neighbouring limb segments, remains a matter for future analysis.

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Chapter 6

Intra- and Interpersonal Movement Coordination in Jointly Moving a Rocking Board

Abstract

In this study, we investigate how two persons (dyads) coordinate their movements when performing cyclical motion patterns on a Rocking Board. In keeping with the Leading Joint Hypothesis (Dounskaia, 2005), the movement dynamics of the collaborating participants were expected to display features of a prime mover with low movement variability. Fourteen subject pairs performed the task in nine amplitude-frequency combinations that were presented in the form of a to-be-tracked stimulus on a computer display. Participants were asked to track the stimulus by jointly rocking the Board sideways while receiving continuous visual feedback of its rotations. Displacements of 28 IREDS that were attached to the Rocking Board, both ankles, knees, hips, shoulders and heads of both actors, were sampled at 75 Hz by means of a 3D-motion tracking system. From these data, we derived body-segment angular excursions as well as the continuous relative phase and time-lagged cross-correlations between relevant joint excursions. The results show that, at the intrapersonal level, knee rotations initially preceded all other joints while the antiphase coordination between the knees displayed relative low variability. At the interpersonal level, dyads adopted a leader-follower strategy with respect to the coordination demands of the task. We take that knee rotations create a dynamic foundation at both intra- and interpersonal levels involving subordination of individual action to joint performance thereby allowing for low-dimensional control of joint action in a high-dimensional, repetitive motor task.

Introduction

Research into between-subject (interpersonal) movement coordination is gradually shifting beyond the exploration of the tacit entrainment of rhythmic motion patterns in tasks that lack any shared action goal. For example, Knoblich and Jordan (2003) have shown in a tracking task that groups possess the ability to use and learn an anticipatory coordination strategy as long as they have access to visual feedback of their co-actor's performance. Recently, we demonstrated in an isometric virtual-lifting task with real-time visual feedback that dyads were capable of resolving redundancy by administering force-sharing synergies (Chapter 4). Even though group performance in these studies was slower than individual performance, the group always performed the task successfully. On the other hand, haptically linked dyads performed significantly faster than individuals on a target-acquisition task (Reed, Peshkin, Hartmann, Grabowecky, Patton & Vishton, 2006). Although dyad members exerted large task-irrelevant counteracting forces, task completion times were systematically lower in dyads (see also Wegner & Zeaman, 1956).

It is well established that in many motor tasks reafferent feedback forms a precondition for successful task performance (Carlton, 1981; Paillard, 1996). Therefore, a possible explanation for less proficient performance by dyads, as compared to individual performance in the aforementioned studies, is that dyads acted on relative slow on-line visual feedback (~135 ms; Carlton, 1981; Saunders & Knill, 2003) of their partners' actions to perceive the consequences of their actions. Higher performance in the latter study could indicate that haptically linked dyads relied on relative fast haptic feedback (~65 ms; Johansson & Birznieks, 2004) to coordinate their actions together.

We reasoned that if the consequences of the co-actor's performance could be picked up haptically, control principles that have been postulated for individual motor control can be applied to joint action. Based on this assumption, we investigated how two *mechanically* linked persons mutually coordinate their movements while performing a repetitive motor task on a Rocking Board (see Figure 1). In general, the Rocking Board is predominantly used in physical rehabilitation for proprioceptive training to enhance stability in stance. The Board compels subjects to channel their many-degrees-of-freedom movement system into a one-degree-of-freedom rocking movement (Bernstein, 1967).

A variety of mechanisms have demonstrated how biological systems, at different levels of control, extract from a large set of available parameters the minimum number of parameters that is needed to act adequately. One strategy is by initially "freezing out" a portion of the available mechanical degrees-of-freedom, i.e. by allowing no or very little movement in a subset of joints (cf. Vereijken et al.,

1992a). Another possibility involves optimization of certain biophysical or behavioral cost function (reviewed in Seif-Naraghi & Winters, 1990). The temporary coupling of actuators into motor synergies by moving two or more joint complexes in close phase relations has been suggested as a strategy in which the central nervous system might solve redundancy (Cole & Abbs, 1986; Santello, Flanders & Soechting, 1998; D'Avella, Saltiel & Bizzi, 2003; Ivanenko, Grasso, Zago, Molinari, Scivoletto, Castellano, Macellari & Lacquaniti, 2003).

Finally, a way in which redundancy is controlled is by relying on hierarchical control. Historically, evidence for action hierarchy has been driven by behavioral experiments (Rosenbaum, 1991) and computational principles (Arbib, Iberall, & Lyons, 1985). Recently, in a review by Grafton and Hamilton (2007), support for action hierarchy has been provided from functional brain imaging studies. In this review, three functional brain imaging studies of action observation using the method of repetition suppression are used to identify a putative neural architecture that supports action understanding at the level of kinematics, object centered goals and ultimately, motor outcomes. These results, based on observation, may match a similar functional-anatomic hierarchy for action planning and execution.

In general, hierarchical control systems rank and organize the control dimensions of a motor task at different levels, where each dimension of the system is a subordinate to a higher dimension and the leading dimension. The advantage of hierarchical control systems is that they include subsystems that can be considered separately from each other, which simplifies the process of control tremendously. In multi-articular limb pointing and reaching movements, Dounskaia (2005) has provided evidence that there is one 'leading-joint' that creates a dynamic foundation for motion of the entire limb. For example, reaching out with the hand to pick-up an object in front of you will also result in movements of the upper and lower arm. These inter-segmental dynamics include internal effects, such as interaction torques emerging as a result of the motion of limb segments. However, the inertia of the hand is considerably less than that of the upper arm and forearm. Consequently, torques at the wrist will have less effect on the motion at more proximal joints (Soechting, 1984). The 'leading-joint' motion generates powerful interaction torques at the other (subordinate) joints. The role of the subordinate control structures is to regulate the interaction torques and to create the net torque that results in the motion of the end-effector required by the task. According to Dounskaia's (2005) Leading Joint Hypothesis (LJH), the 'leading-joint' is responsible for the production of the global characteristics of the limb movement, and largely independent of subordinate joint motion thereby reducing complexity and movement variability. The subordinate joint control is relatively more complicated because it takes into account limb motion produced by the 'leading- joint', which requires continuous coordination of this control with interaction torques that inevitably results in higher movement variability.

In sum, the 'leading-joint' will display features of joint rotations that contribute mainly to end-effector displacements, precede the chain of joints in time, and show low movement variability.

In our present investigation we tested the generality of the LJH in a kinematic analysis of the joint-coordination patterns that dyads displayed while moving a rocking board along a prescribed angle and at an imposed frequency. For within-subject (intrapersonal) interjoint coordination we expected that actors would, after having settled in into the task, quickly resort to a 'leading-joint' coordination strategy. Observations from the Vereijken et al., 1992a study showed that, on average, knee rotations (~47.90 deg) were larger that rotations at the hips (~28.66 deg) and ankles (~23.67 deg) when participants performed slalom-like ski movements on a ski apparatus. Although coupling strength between congruent joint-rotations (hips, knees and ankles) in this study were comparable, we expected that knee rotations, in which an alternation of left and right knee rotations would be the main contributors to displace the lateral movements of the rocking board.

Rather than calculating the propelling and interaction torques separately to identify the prime movers, we reasoned that 1). The amplitude of the joint rotations with an assessment of 2).The maximum cross correlations with associated time-lag of these rotations and 3). An accompanying variability of the continuous relative-phase analysis between congruent body rotations, would reveal which coordination strategy the subjects used. With respect to the within-subject coordination strategy, we expected to be able to identify 'leading-joint' features of within-subject, congruent (e.g. left knee – right knee) joint rotations. Furthermore, in keeping with the Leading Joint Hypothesis predictions we expected for the interpersonal coordination strategy that these 'leading-joint' features are allocated more often to one of the dyads partners thereby revealing a "Leader-Follower" strategy by the mechanically linked collaborating dyads.

Method

Participants

Twenty-eight psychology students from the University of Nijmegen participated in our study. Their age ranged between 22 and 27 years. All participants had normal or corrected-to-normal vision and none had motor problems. All participants gave their informed consent and were rewarded for their participation with either course credits or payment of 12 Euros. Experimental procedures followed the APA guidelines for the ethical treatment of human participants.

Task and Procedure

The participants were randomly paired and given written instructions before the experimental session began. The subject-pairs (dyads) stood on a 200x60 cm wooden Rocking Board with the base pad covered in non-slip surface as customary used in physiotherapy for proprioceptive training (see Figure 1). The board could only rock from side to side in one dimension (x-dimension) with a maximum tilt of 30 degrees to either side. Each participant performed side-to-side rocking

Figure 1.
Side-view of the experimental setup shows two subject pairs standing vis-à-vis on the Rocking Board, performing the task together.

movements in nine conditions spanning three amplitudes (8, 18 and 28 degs) and three frequencies (0.4, 0.6 and 0.8 Hz). Furthermore, the task was executed both individually and as a dyad. When together, they were placed in one of two different stances viz.: vis-à-vis (seeing each other) or back-to-back (not seeing each other). In both conditions, the instructed and realized amplitude-frequency combinations were presented real-time on computer displays (see Figure 2) in the form of rotating bars. Participants were asked to track the indicated movement amplitude and frequency by jointly rocking the board sideways while continuously receiving visual feedback of the actual amplitude and frequency. They were not allowed to talk to each other. Before the experiment started, participants were allowed to practice the task a few times to get comfortable with controlling the movements of the rocking board.

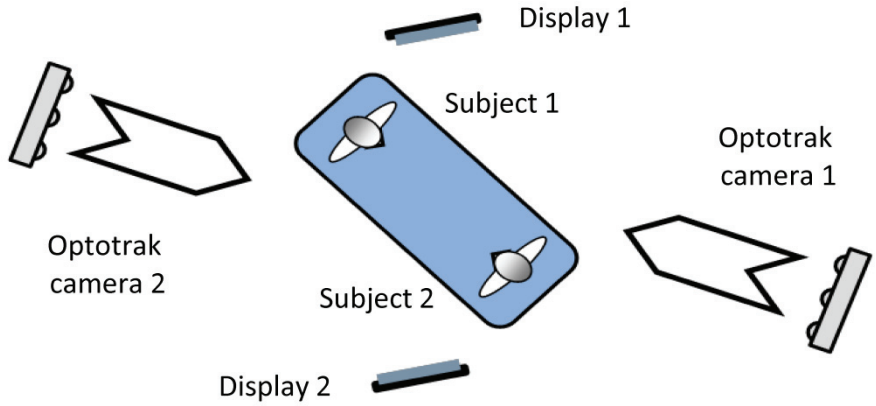

Figure 2.
Schematic top view of experimental setup showing a dyad (subject 1 and 2) standing on the Rocking Board. Two OPTOTRAK cameras were fixed at opposite sides on the walls while facing downward at an angle of 45^{o} relative to ceiling. Two computer displays are placed at eye-level at a comfortable distance off-center to the right of the subject-pair.

Each experimental session consisted of four blocks of 27 trials leading to a total of 108 trials for each session. Each trial lasted 30s. The trial started when the stimulus bar began to tilt and ended when the stimulus bar ceased to rock. Each block consisted of three repetitions of the nine amplitude-frequency combinations that were presented at random. The first and fourth trial block was always a joint-action condition either with participants facing each other or standing back-to-back. In the second and third block, the participants performed the task individually (control conditions). All blocks were counterbalanced across the experiment. Participants never performed more than 54 trials in succession.

Data acquisition

Three rigid bodies were used: one was mounted on the base pad of the rocking board and two were strapped onto the foreheads of each participant. Each rigid body consisted of four infrared light emitting diodes (IREDs) fixated on a flat aluminum plate. In addition, 16 IREDS were attached to the ankles, knees, hips, and shoulders (over the Coracoid process) of each actor. Translations of the IREDS and rotations of the rigid bodies were recorded at a rate of 75 Hz and with a spatial accuracy better than 0.2 mm in the *x, y* and *z* direction by means of a 3D-motion tracking system (Optotrak 3020, Northern Digital Inc., Waterloo, Canada; Figure 2). At the same time, the instructed and realized angular rotations of the rocking board were sampled real-time at a rate of 38.7 Hz and recorded into a separate file.

Data Analysis

All position data were filtered with a second-order Butterworth, zero phase lag, low-pass filter with a cut-off frequency of 6 Hz. The instructed and realized angular rocking movements were resampled to 75 Hz and filtered with a second-order, dual-pass Butterworth filter. The high-pass frequency was 0.5 Hz for these signals and the low-pass cut-off frequency of the filter was also set to 6 Hz. This ensured that an automatic peak-to-peak detection algorithm could be applied reliably. On the basis of this algorithm, successive cycles were extracted of which the first and last cycle of the trial were not included in the analysis.

Kinematics

Extrinsic plane-independent, intrinsic body angular excursions (MJθ in degs) for the left and right body side were extracted off-line from the calculated positions of the twenty-eight IREDs. The head, shoulder, hip, knee and ankle angles were defined as the enclosed angles between two neighboring segments (cf. Vereijken et al., 1992a). Extrinsic plane-independent angular displacements indicate combined rotations in three-dimensional joint space, e.g. increasing angular rotations at the hip joints indicate a combined extension/abduction/exorotation of the hip. An angle of 180 degs at the knee joint indicates full extension.

Time series analysis

Continuous relative-phase time functions and maximum cross-correlation functions with associated time lag were determined for: 1). Within-subject congruent intrinsic body angles (between both shoulders, hips, knees and ankles angles of a participant), 2). Within-subject vertically linked intrinsic body angles (for the left and right body side of a participant) and for the 3). Between-subject congruent intrinsic body angles (between the shoulders, hips, knees and ankles angles of each participant). The means (Mφ in degs) and standard deviations (SDφ in degs) of the continuous relative-phase signals of the relevant joint rotations were calculated by using Batschelet's (1981) procedure involving circular statistics (see Meulenbroek, Thomassen, van Lieshout & Swinnen, 1998). The time lag (ms) was determined by shifting one of the angular displacement functions in time to obtain a maximum cross-correlation value.

The following procedure was applied to our data to provide us with an opportunity to investigate the Leading Joint Hypothesis. First, the time lag of within-subject vertically linked intrinsic body angles was determined per trial. Joint rotations that were leading in time for the duration of each trial were identified and tagged 'leading-rotations' whilst the joints that lagged behind were tagged 'following-rotations'. Next, this information was transferred to both the within-subject and between-subject congruent intrinsic body angles data sets. Thus, we could now

compare the variability of the 'leading-rotations' joints with the 'following-rotations' joints. Finally, we tagged subjects as 'leader' when aforementioned 'leading-joint' features could be allocated more often to them than to their partner ('follower').

The critical value for statistical significance was set at the .05 level. Paired samples t-tests were used to evaluate the statistical significance of observed differences between the incidences of time lags after having tested for normality using the One-Sample Kolmogorov – Smirnov Test to justify using the paired t-test. Repeated measures ANOVAs were applied to evaluate the continuous movement parameters.

Results

Realized amplitudes and frequencies

All participants produced, on average, the instructed movement amplitudes and frequencies well (see Table 1). As expected, the realized amplitudes decreased somewhat as the imposed frequencies increased ($F(2,26)=4.291$, $p<.05$). The reverse was not true, however. The realized frequencies slightly increased as the imposed amplitudes increased ($F(2,26)=4.978$, $p<.05$). We will return to this deviating finding in the discussion.

Table 1.
Left-hand panel: instructed and realized mean amplitudes (standard deviations between brackets) pooled across frequency conditions. Right-hand panel: instructed and realized mean frequencies (standard deviations between brackets) pooled across amplitude conditions.

Amplitude (deg)	
Instructed	Realized
8	10.00 [1.94] **
18	18.06 [2.44] **
28	23.87 [2.83] **

Frequency (Hz)	
Instructed	Realized
0.4	0.41 [0.03] **
0.6	0.61 [0.05] **
0.8	0.80 [0.04] **

** p < .05

Joint amplitudes

Table 2 shows the mean plane-independent angular displacements (MJθ in degs) for all body and Rocking Board rotations as a function of the three imposed amplitudes (8, 18 and 28 degs).

Table 2.
Mean plane-independent angular displacements (MJθ in degs; standard deviations between brackets) for all body and Rocking Board rotations as a function of the three imposed amplitudes (8, 18 and 28 degs).

	8 deg	18 deg	28 deg
Head	2.24 [1.10]	2.55 [1.14]	2.78 [1.16]
Shoulder	2.12 [1.29]	2.52 [1.27]	2.83 [1.30]
Hip	4.48 [2.30]	6.77 [3.17]	8.38 [3.47]
Knee	10.76 [5.14]	19.41 [6.20]	24.36 [7.33]
Ankle	2.32 [1.97]	4.30 [2.99]	5.71 [3.52]
Rocking Board	8.88 [2.21]	15.85 [2.37]	21.14 [3.04]

On average, the angular displacements at the head (M = 2.52, SD = 1.15) and shoulder (M = 2.49, SD = 1.32) were relatively small across the three imposed amplitudes whilst the rotations at the ankle (M = 4.00, SD = 3.17) and hip (M = 6.51, SD = 3.41) were relatively larger than rotations at the head and shoulder, increasing in size with increasing amplitude constraints. Even though the knee's rotation axis was orthogonally oriented to that of the Rocking Board, the knee produced, on average, the largest rotations (M = 18.14, SD = 8.43) that scaled proportionally with the amplitude constraints. These angular displacements at the knee were on average slightly, but significantly, larger than the rotations at the Rocking Board ((M = 15.26, SD = 5.63; $t(27)=3.678$, $p<.05$).

Not only did rotations at the knee closely match the angular displacements of the Rocking Board in size, knee rotations were, as presented in the following results, also mostly ahead in time for all movements.

Coordination dynamics

Figure 3 displays the incidence of number of occurrence of the means (per trial) of the continuous relative-phase time functions (Mφ) for the within-subject congruent body angles. Two distinct coordination modes, in phase (0 degs) and out of phase (180 degs), can be observed between congruent body angles. The top-left panel shows that the isodirectional (same direction) coordination mode (in phase) occurred more often than the non-isodirectional (opposite direction) coordination mode (out of phase) between the shoulder rotations. The top-right panel shows that the opposite was true for the hip rotations i.e., antiphase was the predominant coordination mode. The bottom-left panel displays the coordination modes for the knee rotations. This

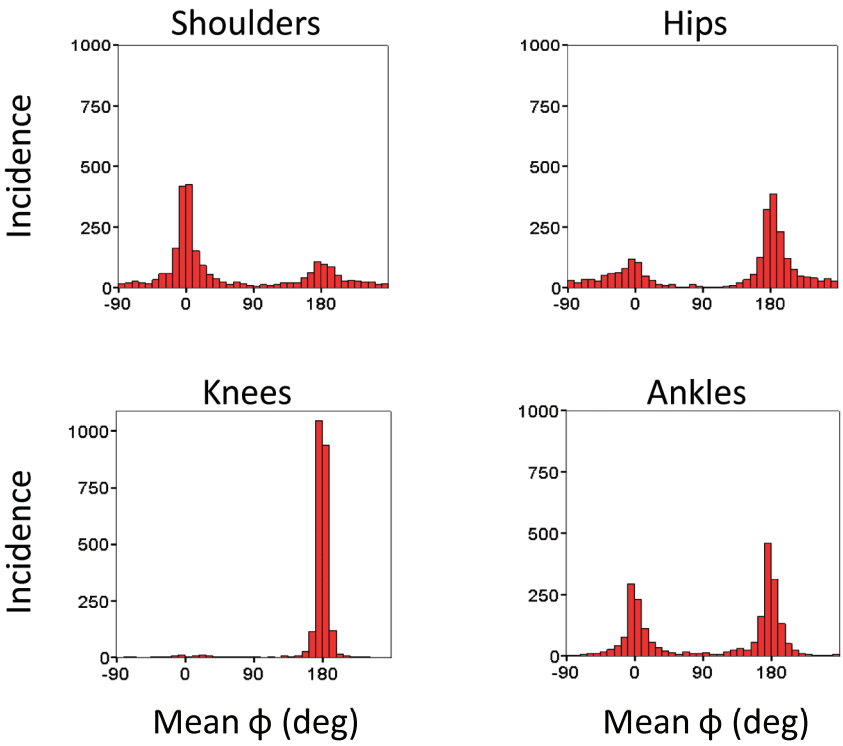

Figure 3.
Histogram displaying the incidence of the Mφ (in degs) for the within-subject congruent body angles. 0 degs indicates in phase and 180 degs indicates out of phase modes.

plot shows that the predominant coordination mode between knee rotations during task performance was non-isodirectional i.e., alternately flexing and extending the knees. The bottom-right panel shows no prevailing coordination mode between ankle rotations.

'Leading-rotations'

The data of the time-lagged cross-correlations for the within-subject vertically linked intrinsic body angles was normally distributed. Figure 4 displays the number of times (in percent) a rotation at a particular location (Head, Shoulder, Hip, Knee and Ankle) led the way in time within the blocked trials (first, second and third, and fourth block) for aforementioned dataset.

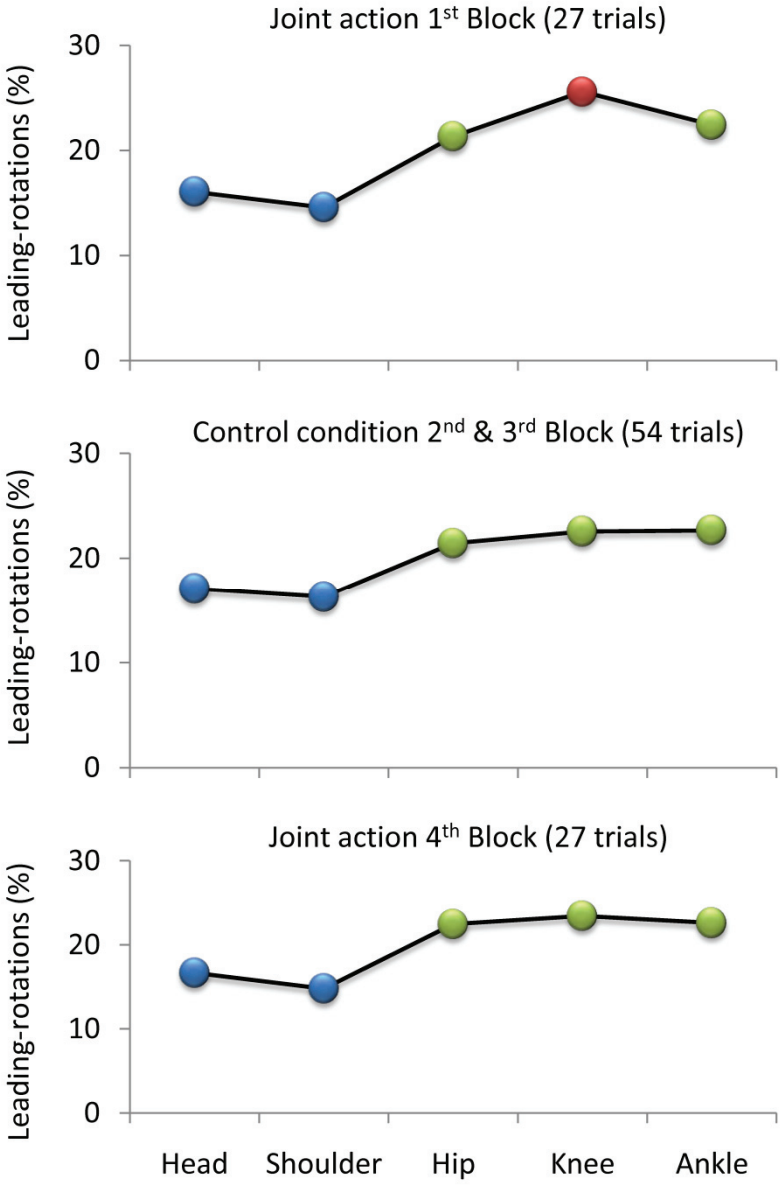

Figure 4.
This Figure displays the number of cases (in percent) a rotation at a particular location (Head, Shoulder, Hip, Knee and Ankle) was ahead in time with respect to the other rotations within the blocked trials (first, second & third, and fourth block).

The top panel of Figure 4 shows, that the incidence for the head (16%) and shoulder (15%) rotations leading the movement were statistically indistinguishable ($t(27)=1.503$, ns). The incidence of hip rotations (21%) ahead in time was significantly higher than the head ($t(27)=6.498$, $p<.01$) and shoulder ($t(27)=7.460$, $p<.01$) rotations. In addition, the ankle rotations (22%) led the way more often than the head ($t(27)=6.713$, $p<.01$) and shoulder ($t(27)=8.103$, $p<.01$) rotations but the incidence between the hip and ankle rotations leading in movement were statistically indistinguishable ($t(27)=0.999$, ns).

Knee rotations led the way in about 26% in all trials with respect to the remaining rotations viz., head ($t(27)=6.419$, $p<.01$), shoulder ($t(27)=9.351$, $p<.01$), hip ($t(27)=3.459$, $p<.05$) and ankle ($t(27)=2.506$, $p<.05$) rotations. In summary, knee rotations preceded other rotations most of the time whilst rotations at the hip and ankle led the way over the head and shoulder rotations.

The middle panel shows the results for the solo action conditions (block 2 & 3) in which the incidence for the head (17%) and shoulder (16%) rotations leading in movement were statistically indistinguishable ($t(27)=.758$, ns). The incidence of hip (21%), knee (23%) and ankle (23%) rotations ahead in time were significantly higher than the head (hip/head; $t(27)=3.890$, $p<.05$; knee/head; $t(27)=3.660$, $p<.05$; ankle/head; $t(27)=4.809$, $p<.01$) and shoulder (hip/shoulder; $t(27)=4.791$, $p<.01$; knee/shoulder; $t(27)=4.750$, $p<.01$; ankle/shoulder; $t(27)=6.293$, $p<.01$) rotations. The incidence of the hip, knee and ankle leading the way were mutual statistically indistinguishable (hip/knee; $t(27)=.770$, ns; hip/ankle; $t(27)=.961$, ns; knee/ankle; $t(27)=.075$, ns). Taken together, rotations at the head and shoulders lagged behind in time to the leading group of rotations (hip, knee and ankle rotations).

The results for the joint condition in block 4 are displayed in the lower panel of Figure 4. This figure shows that the incidence for the head (17%) and shoulder (15%) rotations leading in movement were statistically indistinguishable ($t(27)=1.522$, ns). The incidence of hip (22%), knee (23%) and ankle (23%) rotations ahead in time were significantly higher than the head (hip/head; $t(27)=8.030$, $p<.01$; knee/head; $t(27)=4.842$, $p<.01$; ankle/head; $t(27)=5.010$, $p<.01$) and shoulder (hip/shoulder; $t(27)=8.173$, $p<.01$; knee/shoulder; $t(27)=7.174$, $p<.01$; ankle/shoulder; $t(27)=8.616$, $p<.01$) rotations. Leading angular displacements at the hip, knee and ankle were statistically indistinguishable (hip/knee; $t(27)=.893$, ns; hip/ankle; $t(27)=.137$, ns; knee/ankle; $t(27)=.905$, ns). In summary, rotations at the hip, knee and ankle mostly led the way with respect to the head and shoulder rotations.

Table 3.
Mean SD of the continuous relative-phase signals (SDφ in degs; standard deviations between brackets) of the within-subject (left column) and between-subject (right column) congruent body angles as a function of body rotation (Heads, Shoulders, Hips, Knees and Ankles).

	SDϕ	SDϕ
Heads	-	73.87 [4.63]
Shoulders	63.75 [11.17]	73.28 [5.82]
Hips	58.48 [12.77]	56.86 [14.64]
Knees	42.02 [13.95]	34.93 [17.10]
Ankles	63.29 [13.46]	59.61 [13.70]

Movement variability

Table 3 displays the standard deviations (SDφ in degs) of the continuous relative-phase signals of the within-subject and between-subject congruent body angles during joint action.

Within-subject rotations between the knees displayed relative more stable phase relationships than rotations between the shoulders ($t(13)=10.235$, $p<.01$), hips ($t(13)=9.498$, $p<.01$) and ankles ($t(13)=6.449$, $p<.01$).

The SDφ between the hips were lower than the SDφ between the shoulders ($t(13)=2.751$, $p<.05$) and ankles ($t(13)=2.184$, $p<.05$) whilst the variability of the phase relationships between the ankles and between the shoulders were statistically indistinguishable ($t(13)=.192$, ns).

Variability of the phase relationships for the between-subject congruent rotations between the knees were lower than the variability between the heads ($t(13)=13.681$, $p<.01$), shoulders ($t(13)=13.954$, $p<.01$), hips ($t(13)=8.418$, $p<.01$) and ankles ($t(13)=7.426$, $p<.01$). Noteworthy, the SDφ of the knee rotations was significantly lower between subjects than within subjects ($t(13)=4.782$, $p<.01$). Phase relationships between the hips displayed more stable phase relationships than the SDφ between the heads ($t(13)=9.658$, $p<.01$) and shoulders ($t(13)=8.296$, $p<.01$) whilst the SDφ between the hips and between the ankles were statistically indistinguishable ($t(13)=1.017$, ns). Furthermore, the SDφ between the ankles was lower than the SDφ between the heads ($t(13)=7.689$, $p<.01$) and shoulder ($t(13)=7.336$, $p<.01$) whilst variability of the phase relationships between the heads and between the shoulders were statistically indistinguishable ($t(13)=1.017$, ns).

In summary, the stability of the phase relationships during joint action were highest between the knee rotations for both within-subject and between-subject congruent body angles. In addition, between-subject knee rotations were coordinated relatively more stable than within-subject knee rotations.

Figure 5 displays the standard deviations of the continuous relative-phase signals

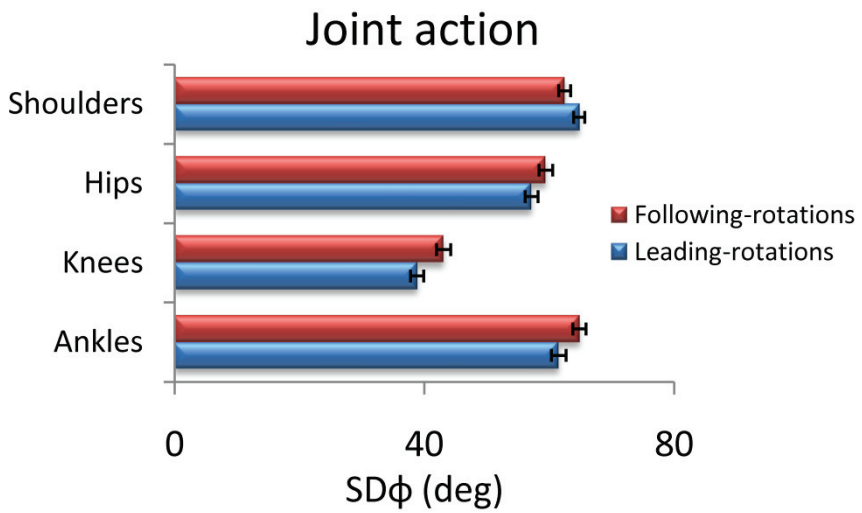

Figure 5.
Bar chart displaying the standard deviations (SDφ in degs) of the continuous relative-phase signals of the within-subject congruent body angles as a function of 'leading-rotations' and 'following-rotations' is shown. Error bars represent 95% confidence intervals.

(SDφ in degs) of the within-subject congruent body angles as a function of 'leading-rotations' and 'following-rotations' (see Method Section).

'Leading-rotations' between the knees (M=39.38; SD=6.88) displayed relative more stable phase relationships than 'following-rotations' (M=43.52; SD=8.48) between the knees ($t(13)=2.833$, $p<.05$). Also the SDφ of the 'leading-rotations' between the ankles (M=61.33; SD=8.42) were lower than the SDφ of the 'following-rotations' (M=64.73; SD=7.09) between the ankles ($t(13)=2.731$, $p<.05$). In contrast, variability of phase relationships between 'leading-rotations' (M=57.14; SD=5.84) and 'following-rotations' (M=59.59; SD=6.75) of the hip were statistically indistinguishable ($t(13)=1.260$, ns) alike the variability of phase relationships between 'leading-rotations' (M=64.87; SD=5.61) and 'following-rotations' (M=62.55; SD=6.32) of the shoulder ($t(13)=1.336$, ns).

'Leader-Follower'

In this last section, we will report the results that allocate prime mover features to individuals. Figure 6 shows the percentage of knee rotations, which led the way whilst displaying low variability of phase relationships between the knees, and assigned to one of the dyads' partners. The top panel shows that, during the first block of 27 joint action trials, one of the partners displayed more features of a 'leader' (~87%) than qualities of a 'follower' (~13%; $t(13)=7.242$, $p<.01$). In the last block of 27 joint action trials, 'leader' features could be allocated more often (~68 %) of the cases to of one partners as opposed to 'follower' features' (~32%; $t(13)=3.679$, $p<.05$).

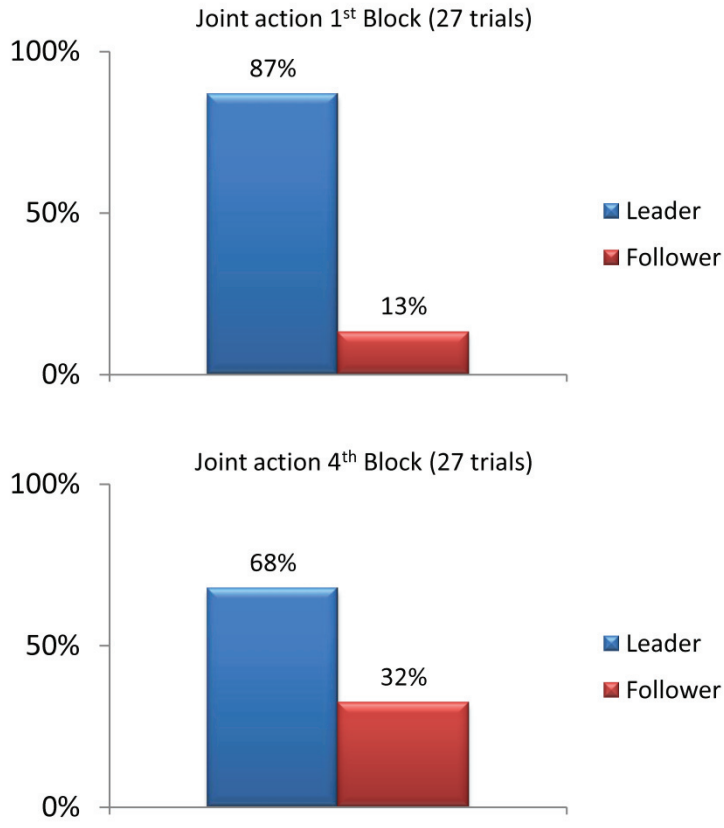

Figure 6.
Bar chart showing the number of cases (in percentage) that knee rotations displaying 'leading-joint' features could be assigned to one of the dyads' partners.

Discussion

In this study, we tested the generality of the Leading Joint Hypothesis (LJH). To this end, we conducted a kinematic analysis of the joint-coordination patterns that two mechanically linked dyads displayed while moving a rocking board along prescribed amplitude and imposed frequency combinations. To execute the side-to-side rocking task on the Rocking Board, participants were confronted with an ill-posed problem, i.e. they were forced to reduce their many mechanical degrees-of-freedom into a one degree-of-freedom rocking movement.

Our observations show that one way dyads controlled redundancy was by relying on hierarchical control at both the intrapersonal and interpersonal coordination level. At the intrapersonal level, we found that knee rotations initially preceded all other joints while the antiphase coordination between the knees displayed relative low variability. A novel finding is that these 'leading-joint' features of the knees provided dyads with a dynamic foundation to perform with respect to the coordination demands of the joint-action task.

The present findings support the generality of the Leading Joint Hypothesis (Dounskaia, 2005), in which knee rotations create a dynamic foundation at both intra- and interpersonal levels involving subordination of individual action to joint performance.

According to the Leading Joint Hypothesis (Dounskaia, 2005), leading joints will at least display the following features viz., be the main contributor to the end-effector displacements, lead the chain of joints in time, and display the lowest movement variability.

Realized amplitudes and frequencies

While rhythmically moving the rocking board sideways, energy optimization most likely prompted the dyads to stick to a general strategy of amplitude undershooting. This is in line with the findings by cf. Gordon et al. (1995). The presently selected movement frequency range elicited overall frequency overshoots, probably because the preferred frequency of the rocking board, with two adults balancing on top of it, was higher than we inferred during the piloting phase of this study. The latter might also be the reason why the realized frequencies increased with an increase of the imposed amplitudes (see Chapter 5).

Joint amplitudes

Relative-phase analysis of intrapersonal, between-congruent body angles revealed that the predominant coordination mode between knee rotations during task performance consisted of alternately flexing and extending the knees (Figure 3). Of course predominantly, because flexion and extension of the knee joint are not simple

hinge movements that occur about a fixed transverse axis of rotation but rather about a constantly changing center of rotation, that is, polycentric rotation. However, knee rotations around the main transverse axis have a normal range of motion (ROM) of about 140 degs, and were found to be, on average, the largest rotations (18 degs) in this task, scaling proportionally with the amplitude constraints, which were slightly larger than the average angular displacements of the Rocking Board (15 degs; see also Table 2). In-phase and out-of-phase were the dominant coordination modes for the intrinsic rotations between the shoulders, hips and ankles. This means that the rotations between these congruent joints were performed simultaneously either in the opposite directions or in the same direction, thereby allowing for a more versatile control structure than for the rotations between the knees. The hip joint is classified as a triaxial joint having movement capabilities around three orthogonally oriented rotation axes. Even though the ROM about the horizontal axis of the hip (~155 degs) is comparable to the ROM of the knee joint around the same axis, hip rotations in this task were nearly three times smaller than knee rotations averaging ~7 degs across the amplitude constraints. The ankle presumably formed the interface between the flexion/extension movements at the knee and sideways rocking movements of the board. Rotations at the ankle joint were on average ~4 degs. Angular displacements at the head (3 degs) and shoulder (3 degs) were, on average, within a small range, stable and increased slightly with increasing amplitude demands.

Kinematic studies in three dimensions of natural or simulated locomotion have shown that head angular displacements in the sagittal plane remain within a range of less than five degs (Pozzo, Berthoz, & Lefort, 1989; 1990; Berthoz & Pozzo, 1988; Pozzo, Berthoz, Lefort, & Vitte; 1991). Head and trunk rotations were also shown to be relatively small and stable in tasks requiring the maintenance of equilibrium on a beam or on a rocking platform (Pozzo, Levik, & Bertoz, 1995). On the rocking platform, the subjects tried to keep the mean angular position of the trunk near the vertical, while the lower limbs behaved like actuators of the head-trunk unit.

Not only did rotations at the knee closely match the angular displacements of the Rocking Board but, as we will discuss in the next section, knee rotations also initially preceded all movements.

'Leading- rotations'

Time lags between intrapersonal vertically linked intrinsic body angles (Figure 4) show that there was a systematic timing order between categories of rotations. In effect, the hip, knee and ankle rotation complex led the rocking movements in about 69% of the time while the head and shoulder complex followed in time.

A popular theory of serial order holds that plans for behavioral sequences are structured hierarchically. According to this theory, the highest-level representation

of a sequence to be produced corresponds to the sequence's main constituents, lower-level representations correspond to lower-level constituents, and so on (Mackay, 1982). An appealing feature of the hierarchical theory is that it accords with the fact that skill learning progresses from simple to more complex routines and that it provides a convenient way of combining and altering movement constituents at different stages (for a review, see Rosenbaum, 1987).

Our observations show that that the behavioral sequences of rotations in the task are embedded in a flexible organization structure that changes in the course of the experiment. Knee rotations in joint performance were, over the first trial block, initially ahead of all other rotations in 26 % of the cases (Fig. 4 top-panel). Rotations of the hip (21%) and ankle (22%) joints led the movement less often than the knee.

Over the last trial block (Fig. 4 lower-panel), rotations at the hip, knee and ankle rotation complex still lead the rotations of head and shoulder complex in 68% cases but rotations at the hip (22%), knee (23%) and ankle (23%) equally played their part in leading the movements. These joint action results over the last trial block are comparable with the data of individual performance (see Fig. 4, middle-panel). Keep in mind that none of the participants had ever seen a rocking board, let alone stand on it, so they were performing a novel task. Participants evidently explored and initially controlled the movement dynamics of the task in the first 27 trials by imposing a preponderant leading-knee strategy. This strategy eventually evolved into a shared modus of hip, knee and ankle rotations leading the way in time. The predominant leading-knee strategy at the outset of the experiment undeniably simplifies the process of control by reducing redundancy but at the same time diminishes flexibility of movement production thereby placing a disproportionate burden on involved structures. We therefore presume that energy optimization most likely prompted dyads to change their initial strategy over time and distribute the load over movement structures by adopting a less stringent hierarchical control system thereby gaining movement flexibility into the bargain.

Now we have identified the hip, knee and ankle rotations as contenders for the position of a leading joint, we will now discuss our findings concerning movement stability of these three possible candidates in which we arrived at the identity of the prime mover.

Movement variability

‘Leading-joint’ control is simple and largely independent of subordinate joint motions. Subordinate joint control, however, is more complicated because it includes limb motion due to the movements of the leading joint, which requires continuous coordination at this control level. Consequently, movement variability will be lower at the ‘leading-joint’ than at the subordinate joints.

Analysis of the standard deviations (SDφ in degs) of the continuous relative-phase signals during joint action show (see Table 3) that the SDφ for within-subject congruent body angles between knees amounted to ~42 degs whilst the SDφ between the hips (58 degs) and ankles (63 degs) were markedly higher. In addition, the SDφ for between-subject congruent body angles between the knees (35 degs) are also lower than the SDφ between the hips (57 degs) and ankles (60 degs).

Noteworthy, the SDφ of the congruent body angles for the knees was significantly lower for interpersonal (35 degs) than for intrapersonal (42 deg) coordination, implying that between-subject knee rotations were coordinated relatively more stable than within-subject knee rotations. This hints at the fact that during joint action participants were attuned in coordinating their actions between each other thereby implying subordination of individual action to joint performance.

We can now confidently point the finger at interactions between knee rotations as stable booster of the rocking movements. However, above results merely reflect features of knee rotations in a general way, i.e. averaged behavior over all trials. In the next section, we will pinpoint features to knee rotations that actually display their prime joint characteristics per trial.

As we have reported in the Method Section, we identified joint rotations that preceded ('leading-rotations') and those that lagged other rotations in time ('following-rotations') and subsequently determined the variability for those phase relationships in congruent joint rotations per trial.

As expected, the standard deviations of the continuous relative-phase signals (SDφ in degs) of the within-subject congruent body angles (Figure 5) showed that knee rotations were coordinated more stable when they were 'leading-rotations' (40 degs) than when they were 'following-rotations' (44 degs). These results show that knee rotations displayed the largest excursions, led the way in time, and were coordinated mutually relatively very stable providing evidence that knee rotations can be regarded as the prime movers in the Rocking Board task.

'Leader-Follower'

Our results show that during the first block of 27 joint action trials, 'leading-joint' features could be tagged in 87% of the cases to one of the dyads partners (see Figure 6). In the last block of 27 joint action trials, these 'leading-joint' qualities could still be allocated in about 68% of the cases to of one of the partners. This means that dyads maintained a "Leader-Follower" strategy throughout the course of the experiment.

The present findings confirm our expectations that control mechanisms for dyads rhythmically moving the rocking board sideways can be modeled in line with principles of the Leading Joint Hypothesis. Dyads displayed leading-joint features at

the intrapersonal level that were subordinate to the “Leader-Follower” strategy at the interpersonal level.

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Chapter 7

Discussion

This chapter contains a discussion of the results of the empirical studies reported in this thesis. Some open problems and suggestions for future research are discussed and we conclude this thesis with formulating a key implication of our research for the clinical practice of physical therapy.

The main purpose of the studies described in this dissertation was to gain more insight into determinants of redundancy management at different levels of motor control. At the same time we sought to identify control principles that transcend the separate views on this subject matter that have been proposed in the field of human motor control. We will now discuss the key findings of our studies within the context of several approaches that we have applied in this dissertation and listed in Chapter 1, viz. coordination, exploitation, allocation and delegation.

Coordination

The Russian physiologist Bernstein (1967) defined coordination as a problem of mastering the many degrees of freedom (DOF) involved in a particular movement, i.e. reducing the number of independent variables to be controlled (Turvey, 1990). Determining the coupling relationship (synergy) between body segments, muscles or joints provides us with insights in the central control signal that jointly and proportionally activates all elements in the synergy. When task demands vary, the control signal to the synergy changes, invoking parallel changes in all elements bound together in the synergy. By extending the notion of synergies to multiple control dimensions, the coordination of multiple DOF may be understood in a similar way (Latash, 2007).

In Chapter 2 we show that the shoulder/elbow synergy (proximal joint-pair) are more strongly coupled than the elbow/wrist synergy (distal joint-pair) when participants performed circular hand movements in the mid-sagittal plane. We find support for our findings because earlier observations have shown that the elbow and wrist are loosely coupled (Lacquaniti, Ferrigno, Pedotti, Soechting & Terzuolo, 1987) whilst the shoulder and elbow are tightly coupled (Soechting, Lacquaniti & Terzuolo, 1986; Lacquaniti, Soechting & Terzuolo, 1986; Lacquaniti et al., 1987). We take that our results reflect two mechanisms that co-determine intrapersonal multijoint control of the arm movements. First, the spring-like properties of bi-articular muscles influence the organization of limb synergies significantly (Gielen, van Ingen Schenau, Tax, & Theeuwen, 1990). Secondly, inertial torques arising

from the shoulder/elbow movements evoke interactive and restraining torques at the more distal joints and are the primary source of elbow/wrist motion. In addition, Dounskaia et al. (1998) found that the main function of wrist-muscle activity was found to intervene with the interactive effects and to adjust the wrist movement to comply with the required coordination pattern in the loosely coupled elbow/wrist joint pair. In sum, our observations in Chapter 2 support the view that the proximal joint pair generates the whole movement but corrections needed to fulfill the task requirements are generated at the distal joint pair (Lacquaniti et al., 1987).

But what is the nature of the central control signal that jointly and proportionally activates all elements in a synergetic performance by two persons when they coordinate their actions to pursue a common goal? To this end, we investigated redundancy control when two people performed an isometric force-production, virtual bar-lifting task (see Chapter 4).

An expected key finding of the study in Chapter 4 is that correlations between supernumerary (redundant) force contributions by dyads performing the task with four hands, during the holding phase, were found to be negative (Figure 4 in Chapter 4). This means that interacting partners not only responded to observed changes but also incorporated the timing of the actions of the partner in their own action planning. Because the contributions to the lifting task by one partner were not directly observable for the other we could effectively rule out that the synchronization of movements between the partners can be molded in accordance with the Haken et al. (1985) model or that performance during the holding phase can be viewed as a compensatory tracking task. Nevertheless, by forming an internal model of the joint-dynamics of the action of which they are part of (cf. Atkeson, 1989; Jordan, 1994) adaptive behavior enabled dyads to generate forces that anticipate rather than merely react to the actions of their counterpart. Our observations show that, during the stabilization phase, each of the actors created a separate synergy by coupling positional changes of bar-ends to control the bar-orientation, and at the same time, these synergies were inversely coupled to jointly control the bar height. This means that the actors did not adopt a joint-action coordination strategy of perfect degree-of-freedom allocation across the participants, i.e., one actor taking care of the height of the bar and the other controlling its rotation.

In conclusion, our results show that the coupling of effectors does not depend on whether the neural control centers of dyads are anatomically linked and confirms earlier suggestions that such synergetic performance by dyads may be informationally and not just anatomically based (Schmidt et al., 1998).

Exploitation

One aspect of redundancy in the multijoint human movement system is that the DOF are dependent on adopted body configurations. For example, the DOF related to the glenohumeral joint is generally constrained by the intra-articular positions both mating surfaces of the joint take up. When conformity between mating surfaces is low, the glenohumeral joint possesses six DOF, i.e. three rotational and three translational DOF. In contrast, when conformity between the male and female surfaces is high, the DOF at the glenohumeral joint is reduced to one rotational DOF.

Our results in Chapter 2 show that this built-in mechanical "joint play" induces a position-dependent variation in inter-joint coordination stability when the circular drawing movements with the hand is performed at certain locations in the mid-sagittal plane. This means that the strong coupling between shoulder and elbow rotations breaks down when conformity between the humeral head and the glenoid is low (Warner et al., 1998; Kelkar et al., 2001).

Not only is the management of redundancy constrained by the biophysical architecture of joints, people in general are very clever in *exploiting* biophysical properties of their motor system. In our study in Chapter 3 we found that when individuals were simultaneously confronted with spatial and temporal constraints in an ellipse drawing task they mostly exploited the intrinsic amplitude-frequency relationships to pursue their goals (41.37%; see Table 2).

It has been demonstrated that the functional use of elasticity is a typical feature of cyclical movements such as produced in tapping tasks (Guiard, 1993). Meulenbroek and Thomassen (1993) also report several findings in the graphic domain which indicate that subjects exploit elasticity of muscles and tendons as a biophysical property of the motor system in the execution of graphic stroke sequences. The finding that subjects initially adopted uncomfortable movement directions and finished in comfortable movement directions corresponds with observations of Rosenbaum and Jorgenson (1992). These authors showed that subjects grabbed the stick in an uncomfortable posture in order to create the opportunity to finish the task in a comfortable posture. One might argue that subjects exploited biomechanical properties of the motor system in selecting the postures that were realized.

Exploiting biophysical properties of the motor system is not the exclusive domain of individual performance. The results in Chapter 5 show that also in joint motor tasks in which two actors coordinate their movements on a Rocking Board, dyads mostly managed to exploit the biomechanical relationships between movement amplitude and frequency when asked to generate specific target values of these parameters (52.64%; see Table 3 in Chapter 5). Given the key role which the visual modality is supposed to play in interpersonal movement coordination (Schmidt & O'Brien,

1997; Richardson et al., 2006), the null results of the study in Chapter 5 indicate that the adopted parameter-change strategy did not vary as a function of whether the participants saw each other while performing the task or not and are, in our view, informative (cf. Harcum, 1990). They demonstrate that exploitation of biomechanics in goal-directed task performance is a prominent motor control mechanism that seems to be independent of the modalities used for monitoring the perceptual consequences of the generated motion patterns.

Allocation

It is conceivable that motor performance is not always efficient or optimal because actors trade biomechanical efficiency for goal attainment. Our results show in the individually performed ellipse drawing task (Chapter 3) and the jointly performed Rocking Board task (Chapter 5) that an appreciable number of movements reflect deliberate control because the resulting movements entailed overriding natural amplitude-frequency relationships to attain their target parameters viz., 30.08% in the ellipse drawing task (Table 2 in Chapter 3) and 26.95% in the Rocking Board task (see Table 3 in Chapter 5).

Trade-offs are common in everyday life. We often select jobs we enjoy at the expense of jobs that reap larger salaries, we live where we do for practical reasons even though we might fantasize about living on a tropical island, and so on. In everyday performance, we likewise trade some values for others. We trade speed for accuracy (Fitts, 1954) or we trade biomechanical efficiency for adherence to required rhythms (Yu, Russell, & Sternad, 2003). Understanding how such trade-offs are managed is a fundamental goal for research on redundancy management.

One way trade-offs *might* be managed is to allocate weights to the dimensions on which performance vary. If speed and accuracy are two such dimensions, then emphasizing speed more than accuracy, say, can be achieved by assigning more weight to speed than to accuracy. One difficulty is, however, that the dimensions being traded may be incommensurate. Speed and accuracy, for example, may have different units, making it unclear how more weight can be assigned to one dimension than the other. Another difficulty with weighting is that it is hard to provide a principled account of trying to do well on more than one dimension at a time. Clearly, high speed along with high accuracy may come with practice (Elliott, Hansen, Mendoza, & Tremblay, 2004), but motivation can also promote high speed *and* high accuracy. The problem of incommensurability of dimensions may, however, vanish at the neural level where weighing of task goals must take place in other dimensions than in which we normally specify motor control parameters.

Weighting of different performance criteria is used in a theory of motor control (Rosenbaum et al., 2001), who proposed an alternative approach. According to the theory, people approach a motor task by formulating, either explicitly or implicitly, a

constraint hierarchy, or prioritized list of task requirements, to be satisfied. Finding solutions to complex problems by relying on constraint hierarchies is widely accepted in decision research, where eliminating possible solutions based on their ability to satisfy ever more specific requirements is known to be effective (Tversky, 1972).

Delegation

In Chapter 6 we carried out a study in which we tested the generality of the Leading Joint Hypothesis (LJH; Dounskaia, 2005).

Dounskaia (2005) elaborated on previous studies (e.g., Lacquaniti, Ferrigno, Pedotti, Soechting & Terzuolo, 1987; Soechting, Lacquaniti & Terzuolo, 1986; Lacquaniti, Soechting & Terzuolo, 1986) and showed that the leading joint is responsible for the production of the global characteristics of the limb movement, and largely independent of subordinate joint motion thereby reducing complexity and movement variability. The subordinate joint control is relatively more complicated because it takes into account limb motion produced by the leading joint, which requires continuous coordination of this control with interaction torques that inevitably results in higher movement variability. To this end, we conducted a kinematic analysis of the joint-coordination patterns that two *mechanically* linked dyads displayed while moving a rocking board along prescribed amplitude and imposed frequency combinations.

From the acquired data, we derived body-segment angular excursions as well as the continuous relative phase and time-lagged cross-correlations between relevant joint excursions.

The normal range of motion (ROM) at the ankle joint for inversion (0-35 deg) and eversion (0-25 deg) should not present a constraint for an ankle-strategy to be adopted in which small lateral shifts of the center of mass of the body are generated by laterally moving the entire body around the ankles, i.e., the lowest hinges in the chain of joints. However, our results (see Table 2 in Chapter 6) show that rotations around the ankle amount to an average of 4 degrees across amplitude constraints. This means that about 23% of the average 18-deg side to side movements of the Rocking Board can be accounted for by ankle rotations. We therefore infer that participants did not predominantly pursue an ankle-strategy.

In contrast, our observations in Chapter 6 show that at the intrapersonal coordination level knee rotations were the main contributor to the Rocking Board movements (see Table 2), initially preceded all other joints (Figure 4) while the antiphase coordination between the knees (Figure 3) displayed relative lowest variability (Left column of Table 3). These observations provide evidence that knee rotations can be regarded as the prime movers in the Rocking Board task.

Furthermore, our results show (see Figure 5) that the within trial coordination stability between knee rotations were lower for knees that lead the way in time (leading-rotations) than for knees that lagged in time (following-rotations). A novel finding is that these 'leading-joint' features of the knees could be assigned more often to one of the dyads partners (Figure 6). These findings support the generality of the Leading Joint Hypothesis (Dounskaia, 2005), in which knee rotations create a dynamic foundation at both intra- and interpersonal levels involving subordination of individual action to joint performance.

Limitations and Future Research

In this section we describe a few limitations of our study and suggest potential future fundamental as well as applied research of redundancy management at multiple levels of motor control.

Limitations

A first limitation of our studies concerns the artefacts of preprocessing digitized motion data. The description of human motion typically necessitates that we obtain measures of the displacement, velocity, and acceleration of the body of interest. However, in the presence of noise incurred during experimentation, differentiation of raw displacement data will yield inaccurate velocity and acceleration values (Pezzack, Norman & Winter, 1977). In order to obtain reasonable derivatives in our studies, raw displacement data were subjected to smoothing by means of the Butterworth digital filter prior to differentiation. Owing to mathematical constraints, the Butterworth digital filter is susceptible to endpoint error in higher derivative data, i.e. erratic behavior at the beginning and end of the computed acceleration data. To avoid these artefacts we excluded the first and last cycle of each trial in the analysis. With this choice potentially interesting motion phenomena were left unnoticed.

From a perspective based on dynamical systems, it has been argued that pooled group data have limited value, prompting Kelso (1995) to point out that: Because each person possesses his or her own "signature", it makes little sense to average performance over individuals (p. 147). In this dissertation we aimed at establishing laws of action that are generalizable to a population and therefore preferred to conduct statistics on outcome or error data with pooled group data as opposed to individual analyses of kinematics. However, to meet these objections we have also provided individual performance data in order to highlight within individuals the complex processes governing motor control (e.g. Figure 7 in Chapter 2; Figures 2 and 3 in Chapter 4).

Future research

A striking observation of the study in Chapter 2 is that the fluency of the circular hand movements in task space were not affected by variations in joint mobility due to low glenohumeral conformity, i.e. positional-dependent laxity of the glenohumeral joint. We hypothesized that this result could be attributed to: (1) the "looseness" of the distal joint coupling overcomes effects of proximal joint variations, (2) proximal joint variations are "filtered out" by adjusting limb stiffness (Van Galen & van Huygevoort, 2000) before they affect the distal joint pair or (3) proximal joint variations are actively compensated.

It stands to reason to assume that these adaptive measures could prove to be insufficient if the global laxity of the glenohumeral joint is increased as is the case in multidirectional instability of the shoulder.

In general, multidirectional instability is characterized by symptomatic global laxity of the glenohumeral joint and may present either traumatically, atraumatically, unilaterally, bilaterally, or with or without generalized joint laxity. Individuals who possess multidirectional instability subluxate or dislocate anteriorly, posteriorly, or inferiorly with concurrent reproduction of symptoms in at least two directions. Symptoms typically are associated with the midrange positions of glenohumeral motion and often occur during activities of daily living. Barden et al. (2004) have shown in an upper limb repositioning task that subjects with multidirectional shoulder instability show significantly greater hand position error than control subjects. Furthermore, the results show that interrepetition error for subjects in both groups improve significantly during the first three movement cycles. These results suggest that after movement initiation, dynamic proprioception is a factor in improving hand position accuracy in both groups, but to a lesser degree in subjects with multidirectional instability. Consequently, subjects with multidirectional instability may have a reduced capacity to use proprioception to refine and control the motor output of the upper limb.

It would be worthwhile to perform an experiment in which subjects with a diagnosed multidirectional instability of the shoulder and controls perform the task as described Chapter 2. By determining the deterioration of the circular hand movements (see Verschueren et al., 1999) and the pressure applied on the drawing board as an indirect measure of limb stiffness (Van Gemmert & Van Galen, 1997) we should be able demonstrate that subjects with a diagnosed multidirectional instability of the shoulder will display deterioration of the circular hand movements and higher limb stiffness than controls because of the inability of the motor system to compensate for increased variability due to the global laxity of the glenohumeral joint. Both, the deterioration of the circular hand movements and higher limb stiffness could serve as a measure by which the gravity of the multidirectional instability affection can be

indexed. In addition, repeated outcome measures over time can be used to monitor the progress of interventions.

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Epilogue

In the prologue we have noted that human sciences should not only answer *how* and *why* a phenomenon occurs, but also try to understand the *purpose* of a phenomenon. Whilst the acquisition of such knowledge is assumed to be an adequate and worthy objective for an academic discipline (Henry, 1964), the acquisition of the knowledge in the academic discipline of physical therapy is assumed to be a requirement necessary for *application* of its professional practices and for the improvement of its professional services (Winstein, Wing, & Whitall, 2003).

In this dissertation we have reported a series of experiments on redundancy management without addressing in any way how behavioral research in general and redundancy management in particular can help the physiotherapeutic community to weigh their options during clinical reasoning. In closing this thesis I will try to fill this gap by translating the insights obtained in the series of studies reported in this thesis to a specific clinical problem.

Let us consider the contribution of physical therapy in the recovery following a total hip replacement (THR) using the posterior approach as a surgical treatment option for advanced osteoarthritis (OA) of the hip[7]. In general, the changes that happen with OA cause the affected hip to feel stiff and tight due to a loss in its range of motion. Bone spurs will usually develop, which can also limit how far the hip can rotate. Thus, preoperative symptoms as a result of severe arthritis of the hip joint commonly include, hip pain, stiffness of the joint, loss of motion and decreased ability to bear weight on the hip. During a THR, the head of the femur is removed and replaced with a metal implant. The joint socket has all of the remaining cartilage and some of the bone removed and replaced with a plastic cup. As many as 16.000 people in The Netherlands undergo this surgical treatment every year.

The physical therapist will work in a variety of settings towards gaining as much function as possible. The interventions are commonly aimed at facilitating transfers and balance in standing upright, increasing the range of motion (ROM) of the hip, strengthening both legs, increase walking distance with or without an appropriate assistive device and initially guarding “hip precautions” i.e., prohibit motions such as crossing the legs, bending down to far or rolling the affected leg inward.

The above example reflects a typical physical therapeutic approach in the recovery following a THR that is based on medical-physiological practice guidelines. Let us now consider a physical therapeutic approach in the recovery following a THR based on medical-physiological as well as neurocognitive arguments.

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[7] Our consideration is also applicable to the recovery following a total knee replacement.

Besides facilitating transfers and balance in standing upright, increasing the range of motion (ROM) of the hip, increasing walking distance and initially guarding "hip precautions", we will focus on two interventions that will enhance motor performance following a THR viz., interventions aimed at coordination and exploitation of the motor system.

Coordination

Apart from the discomfort due to surgical treatment, subjects are relieved from preoperative symptoms that resulted from the severe arthritis of the hip joint. In addition, subjects are usually allowed to bear full weight on the hip implant within 24 hours after surgery. Typically, subjects are hesitant to stand and walk without an appropriate assistive device. Understandably so, because a portion of the degrees-of-freedom at the hip joint was "frozen" as a result of OA and directly after THR the degrees-of-freedom are suddenly reintroduced into the motor system and must now be incorporated (again) into larger coordinative structures.

One way we can facilitate the process of reorganizing redundancy is by means of the Rocking Board task as described in Chapter 5 and 6. Off course, precautionary measures like wearing an overhead harness will have to be implemented to prevent the subject from falling off the Rocking Board. When the physical therapist takes on the role of "leader" in the jointly performed side-to-side rocking movements, he/she can safely constrain hip rotations of the subject (see Table 2 in Chapter 6) within an average range of 7 degrees by controlling the sideway excursions of the Rocking Board and at the same time impose symmetrical side-to-side rocking movements. These measures will allow the subject to regain confidence in shifting body weight onto the legs and, if necessary, compel the subject to apply weight on both hips. Furthermore, the task offers the subject to relearn a versatile control mode for the hips (see Figure 3 in Chapter 6). Variability of practice can be achieved by varying amplitude and frequency of the side-to-side rocking movement and by varying the stance on the Rocking Board whilst knowledge of results is displayed on the computer displays in the form of rotating bars. Once the subject is comfortable with the Rocking Board movements, solo performance by the subject with imposed amplitude/frequency parameter combinations can be considered a viable option to further motor performance.

Furthermore, to monitor and gather the data of the realized movement amplitude and frequency of the Rocking Board we propose the use of a triaxial accelerometer e.g. the Dynaport^{MiniMod} TriAcc. The TriAcc with a sample rate of 100 Hz and a resolution of 1mg ($1g = 9.8 m/s^2$) contains three orthogonal placed piezo-capacitive acceleration sensors. An accelerometer is a practical, time saving and cost-effective recording device for clinical use.

Exploitation

In Chapter 3 we demonstrated that at low movement speeds participants can pursue multiple movement goals simultaneously, but at higher movement speeds their capacity to satisfy multiple task goals is reduced. This means that, in the aftermath of a THR, walking with low movement frequency will allow the subject to adopt a deliberately controlled movement pattern. However, by pursuing higher walking speeds, the subject will be forced to exploit the biophysical properties of their motor system thereby enhancing efficient, flexible, reliable and robust motor performance.

We find support for our approach to emphasize redundancy management in a series of related studies (Rudolph, Eastlack, Axe, & Snyder-Mackler, 1998; Rudolph, Axe, & Snyder-Mackler, 2000; Rudolph, Axe, Buchanan, Scholz, & Snyder-Mackler, 2001) in which movement patterns between groups of anterior cruciate ligament (ACL) deficient subjects were investigated. Kinematic and kinetic differences between patients who compensated well for the injury (copers) and those who require operative stabilization (non-copers) after anterior cruciate ligament injury (ACL) were compared. The results of these three studies indicate that copers used joint kinematics similar to those of their uninvolved knees and similar to knee motions reported in uninjured subjects. In contrast, non-copers consistently demonstrated less knee flexion in the involved limb that did not correlate directly with quadriceps femoris muscle weakness. Non-copers also achieved peak hamstring activity later in the weight acceptance phase and used a strategy involving more generalized co-contraction. The data suggest that non-copers utilize a stabilization strategy which stiffens the knee i.e. a strategy of general co-contraction with a greater relative contribution from the hamstring muscles. However, neither the copers nor the non-copers showed evidence that quadriceps activation was diminished.

Further evidence for our approach is provided by observations in longitudinal studies showing that strength training of the knee extensors improves strength but does not improve fluctuations in motor output (Bellew, 2002; Tracy, 2001). In contrast, training protocols that emphasize muscle coordination and skill improve the consistency of motor output in various muscle groups (Christou, Yang, & Rosengren, 2003; Ranganathan, Siemionow, Sahgal, Liu, & Yue, 2001; Yan, 1999).

Considering these findings, we propose that a physical therapeutic approach based on medical-physiological as well as neurocognitive arguments in the recovery following a THR should be aimed at facilitating transfers and balance in standing upright, increasing the range of motion (ROM) of the hip, increasing walking distance, initially guarding “hip precautions” and the management of regained DOF via coordination and exploitation of the motor system.

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Summary

In this thesis we address an important research topic in cognitive neuroscience, i.e. how we manage the excess of resources in our motor system that allows us to perform a movement task in numerous different ways. Such redundancy or abundance of possible solutions to achieve a selected goal improves the reliability and flexibility of our motor system and potentially provides us with an unsurpassed adaptability in performing daily life activities. However, redundancy becomes a problem when we try to fathom the mechanisms underlying the management of the degrees of freedom (DOF) of the motor system.

The introduction to the thesis presents a taxonomic outline of different approaches in the literature that describe how the DOF problem, as it appears in the field of human motor control, can be solved. These include: (1) the elimination or reduction of the degrees of freedom to the ones necessary to perform the task (elimination), (2) the temporary coupling of actuators into motor synergies (coordination), (3) applying the tools of optimal control theory (optimization), (4) the view that adaptive motor behavior entails exploitation of, rather than resistance to, biomechanical properties (exploitation), (5) that different tasks can be defined by different constraints, or the order of the same constraints may vary depending, for example, on whether grace, speed, or accuracy is most important (allocation) and (6) the approach that plans for behavioral sequences are structured hierarchically (delegation).

In the five subsequent empirical chapters we tested predictions derived from several of the aforementioned research positions at different levels of motor control, viz. interjoint, parameter and force level in intra- and interindividual control of action.

The first study addresses intraindividual motor control at the level of individual joints during a drawing task. The main finding confirmed earlier observations that in sagittal-plane movements the shoulder and elbow are more strongly coupled than the elbow and wrist. However, the built-in mechanical 'joint play', a typical characteristic of the architecture of the shoulder joint, was shown to induce a position-dependent variation in interjoint coordination stability that, to date, has been neglected.

In the second study we examine intraindividual motor control at the movement parameter level. In a loop writing task we adopted a novel approach in that we tried to infer deliberate control from the kinematics of the pen-tip movements being generated under controlled conditions. The *paradigm* we applied is based on observations that large-amplitude arm movements tend to be performed at low frequencies by means of shoulder and elbow rotations, whereas small-amplitude arm movements tend to be performed at higher frequencies through wrist and finger rotations. Asking participants to depart from these habitual movement patterns requires them to refrain from relying on intrinsic amplitude-frequency relationships

and, in its stead, to activate less natural, possibly more attention-demanding, control regimes. The findings demonstrated that at low movement speeds the participants were able to pursue multiple movement goals simultaneously but that at higher speeds their capacity to satisfy multiple task goals was significantly reduced.

The study reported in the third study uses a virtual force-lifting test to determine how people coordinate forces when they need to perform a task together that could also be performed alone. We found interindividual force synergies that were brought about by the adaptive processes involved in the joint execution of the task that reflect each actor's ability to simulate the partner's actions.

In the fourth and fifth studies we exploited a rocking board task to investigate intraindividual and interindividual control when people are mechanically coupled. In the first of the two studies we address the key role the visual modality is assumed to play in interindividual movement coordination. We focused on the relative amount of predictive motor control in conditions in which the two participants stand face-to-face (i.e. being able to observe one another) and back-to-back (i.e. being unable to see each other). We additionally expected that when people are simultaneously confronted with spatial and temporal constraints in this repetitive motor task, they would either exploit the biomechanical amplitude-frequency relationships or adopt a cognitive strategy to control frequency and amplitude. The results demonstrated that exploitation of biomechanics in goal-directed task performance is a prominent motor control mechanism that seems to operate independently of the modalities people use to monitor the perceptual consequences of the generated motion patterns.

In the second of the two rocking-board investigations we tested the generality of the Leading Joint Hypothesis (LJH) in a kinematic analysis of the joint-coordination patterns that dyads display when they need to manipulate a rocking board along a prescribed angle and at an imposed frequency. We found knee rotations to create a dynamic foundation at both intra- and interindividual levels involving subordination of individual action to joint performance to allow for low-dimensional control of joint action in this high-dimensional, repetitive motor task.

In the final chapter we discuss the results of the empirical studies reported in this thesis within the context of the various approaches that we pursued in the course or our investigations, viz. coordination, exploitation, allocation and delegation. We further touch on some open problems and offer suggestions for future research. The thesis concludes with a key implication of our research for the clinical practice of physical therapy.

In conclusion, the studies reported in this thesis show that the management of redundancy is not only constrained by the anatomical make-up of our effector system but that, in general, we are very clever in exploiting the biophysical properties of our motor system and can deliberately trade off biomechanical efficiency for goal attainment. Furthermore, the studies demonstrated that control

principles that have been postulated for individual motor control are also applicable to joint action. The present findings have potential implications for physical therapy, which are discussed in detail.

Samenvatting

In dit proefschrift wordt een belangrijk onderzoeksthema uit de cognitieve neurowetenschappen behandeld, te weten: hoe wij de overvloed aan vrijheidsgraden van ons bewegingsapparaat aansturen en benutten waardoor we in staat zijn een bewegingstaak op verschillende manieren uit te uitvoeren. Een dergelijke redundantie van oplossingen verhoogt weliswaar de betrouwbaarheid en flexibiliteit van ons bewegingsapparaat en zorgt voor een onovertroffen aanpassingsvermogen bij de uitvoering van onze dagelijkse activiteiten maar vormt een probleem als we de onderliggende mechanismen die de vrijheidsgraden van het bewegingsapparaat beheersen trachten te doorgronden.

De inleiding van het proefschrift beschrijft een taxonomie van verschillende benaderingen in de literatuur waarmee het vrijheidsgradenprobleem opgelost kan worden. Deze zijn: (1) het terugbrengen van vrijheidsgraden tot die welke strikt noodzakelijk zijn om een taak uit te voeren (eliminatie), (2) de tijdelijke koppeling van mechanische vrijheidsgraden in bewegingssynergieën (coördinatie), (3) het toepassen van optimalisatieprincipes van bewegingssturing (optimalisatie), (4) de exploitatie van biomechanische eigenschappen (exploitatie), (5) dat taken gedefinieerd kunnen worden door hun beperkingen en dat het relatieve belang van deze beperkingen kan variëren afhankelijk van de bewegingsdoelen, bij bijvoorbeeld gratie, snelheid of accuratesse (allocatie) en (6) de benadering dat actieplannen hiërarchisch gestructureerd zijn (delegatie).

In de vijf opeenvolgende empirische hoofdstukken worden voorspellingen getoetst vanuit verschillende van de bovengenoemde invalshoeken op uiteenlopende niveaus van bewegingscontrole, te weten: tussen gewrichten, parameter- en krachtniveau tijdens intra- en inter-individuele controle van acties.

De eerste studie richt zich op intra-individuele bewegingscontrole op het niveau van armgewrichten tijdens het uitvoeren van cyclische bewegingen van de hand. De belangrijkste bevinding bevestigt eerdere observaties dat tijdens bewegingen in het sagittale vlak, de schouder en de elleboog sterker gekoppeld zijn dan de elleboog en de pols. Echter, de inherente mechanische bewegingsspeelruimte die een typisch kenmerk is van de architectuur van het schoudergewricht veroorzaakt een positieafhankelijke variatie in de stabiliteit van de coördinatie in het anders zo sterk gekoppelde schouder/elleboog bewegingspaar. Deze observatie is tot op heden onopgemerkt gebleven.

In de tweede studie onderzoeken we bewegingscontrole op parameterniveau. Tijdens een opdracht waarbij guirlandes geschreven dienen te worden passen wij een nieuwe benadering toe waarbij, onder gecontroleerde condities, intentionele controle wordt afgeleid uit de kinematica van de penbewegingen. Het paradigma dat we hebben

toegepast is gebaseerd op de observatie dat grote armbewegingen normaliter in lage bewegingsfrequenties worden uitgevoerd met behulp van schouder- en elleboogrotaties terwijl kleine armbewegingen in hogere bewegingsfrequenties worden uitgevoerd door pols- en vingerrotaties. De vraag aan proefpersonen om af te wijken van dit gebruikelijke bewegingspatroon, vereist dat ze niet meer kunnen vertrouwen op de intrinsieke amplitude/frequentie relaties maar daarvoor in de plaats minder natuurlijke controle regimes dienen te activeren die daardoor mogelijk meer aandacht vragen. De onderzoeksresultaten laten zien dat de deelnemers in staat waren om bij lage schrijfsnelheden meerdere taakdoelen tegelijkertijd na te streven, maar dat bij hogere schrijfsnelheden het vermogen om tegelijkertijd aan meer dan één taakdoel te voldoen was verminderd.

De studie in het derde hoofdstuk gebruikt een virtuele tiltaak om te bepalen hoe mensen isometrische krachten coördineren als ze een taak gezamenlijk moeten uitvoeren die ook alleen uitgevoerd kan worden. Wij vonden dat inter-individuele krachtsynergieën veroorzaakt werden door adaptieve processen tijdens de gezamenlijke taakuitvoering die het vermogen van de deelnemers om elkaars acties te simuleren weerspiegelen.

In de vierde en vijfde studie hebben wij een schommelbord gebruikt om intra- en inter-individuele controle te onderzoeken wanneer mensen mechanisch zijn gekoppeld.

In de vierde studie bekijken wij de sleutelrol die de visuele modaliteit speelt in inter-individuele bewegingscoördinatie. Hierbij hebben we ons specifiek gericht op de mate waarin twee deelnemers tot proactieve bewegingssturing in staat zijn wanneer zij met de gezichten naar elkaar toe staan (elkaar zien) of waneer ruggelings staan (elkaar niet zien). Wij verwachtten dat wanneer mensen in deze repeterende bewegingstaak tegelijkertijd geconfronteerd werden met spatiële en temporele restricties, ze of 1) de biomechanische amplitude/frequentierelaties zouden exploiteren of 2) een cognitieve strategie zouden aanwenden om amplitude en frequentie te controleren. De resultaten geven aan dat het gebruik van biomechanica bij een doelgerichte taakuitvoering een prominent bewegingscontrolemechanisme is dat onafhankelijk lijkt te opereren van de modaliteiten die mensen aanwenden om de zintuiglijke consequenties van gegenereerde bewegingspatronen te controleren.

In de vijfde studie hebben wij de generaliteit getest van de zogenaamde ‘Leading Joint Hypothesis’ (LJH; Dounskaja 2005) in een kinematische analyse van de gewrichtscoördinatiepatronen die dyades (tweetallen) produceren als een zij een schommelbord moeten bewegen in een voorgeschreven hoek en met een opgelegde frequentie. Wij vonden dat knierotaties de dynamische basis vormen voor bewegingen op intra- en inter-individueel niveau met een ondergeschikte rol voor individuele acties. Deze taakverdeling maakt het mogelijk om deze hoogdimensionale repeterende bewegingstaak laagdimensionaal aan te sturen.

In het laatste hoofdstuk van dit proefschrift worden de resultaten besproken van de empirische studies binnen de context van de verschillende benaderingen die wij in de loop van onze onderzoekingen hebben toegepast, te weten: coördinatie, exploitatie, allocatie en delegatie. Verder gaan we in op enkele algemeen bekende vraagstukken op het terrein van bewegingssturing en geven we suggesties voor relevant vervolgonderzoek. Het proefschrift eindigt met een sleutelimplicatie van ons onderzoek voor de klinische praktijk van fysiotherapie.

Samenvattend laten de studies gebundeld in dit proefschrift zien dat het beheersen van redundantie niet alleen bepaald wordt door de anatomie van ons effectorsysteem, maar dat mensen heel slim de biofysische eigenschappen van hun bewegingsapparaat weten te benutten en uit te buiten en bewust biomechanische efficiëntie opofferen t.b.v. doelgerichtheid. Verder hebben de studies laten zien dat modellen voor individuele bewegingscontrole ook toepasbaar zijn voor gezamenlijke acties. De huidige bevindingen hebben mogelijke implicaties voor de fysiotherapie, welke in detail besproken zijn.

摘要

本文将重点讨论认知神经科学中的一个重要课题，即人体如何管理运动系统的过多资源，以便能以多种不同方式执行某种运动功能。实现某个既定目标时可供使用的可能方案如此之多，不仅提高了人体运动系统的可靠性和灵活性，也使人体在从事日常活动时有可能具有高超的适应性。但是，当我们需要理解运动系统自由度（DOF）的管理机制时，过多的资源就成了一种负担。

本文前言部分将分门别类地概要介绍相关文献中记载的不同方法，这些文献介绍了人体运动控制系统是如何解决自由度问题的。具体方法包括：（1）消除或降低自由度，只留下那些执行某项功能所必须的（消除法）；（2）临时耦连各施力者，使之形成运动协同（协调法）；（3）应用最优控制理论工具（优化法）；（4）调查适应性运动行为如何利用（而不是妨碍）生物力学特性（利用法）；（5）由不同的限制性因素或相同限制性因素的顺序所规定的不同任务，会因为执行该任务时优美、速度或准确是否重要而有所不同（分配法）；（6）按层次排列规划行为顺序的方法（授权法）。

在以下五个观察性章节中，我们在不同的运动控制水平检验了根据某些上述研究结论所得出的预测。这些是指关节间、参数和力量水平的单个被试者的自身行为和各被试者的行为。

第一项研究讨论的是绘画时各关节的动作控制。结果证实了早期的观察，即在矢状面运动时肩肘间的耦连强于肘腕间的耦连。但研究发现，由于内在的机械性'关节内动作'（肩关节的一种典型结构特征），关节间的协调稳定性会随姿势而变化。至今为止，这一点一直被忽略了。

在第二项研究中，我们在运动参数水平检验了单个被试者的动作控制。在被试者画圆圈时，我们采用了一种全新的方法。我们试图根据控制条件下的笔尖运动来推断有意控制。我们所采用的*范例*是基于某些观察结果。根据这些观察，上肢的大幅度运动是通过肩肘关节低频率旋转实现的，而上肢的小幅度运动则是通过腕关节和手指高频率旋转实现的。我们要求被试者放弃这些习惯性动作，不要依赖内在幅度-频率关系，而采取不太自然的可能需要更多注意力的控制方式。结果发现，做低速动作时，被试者能够同时完成多项运动，但在做高速动作时，他们同时完成多项运动的能力明显下降。

第三项研究采用了一种虚拟举重测试，以检验被试者在一同完成一项可单人完成的任务时的协调情况。我们发现被试者之间有力量协同现象。力量协同任务涉及到关节的适应性过程，反映了被试者模拟他人动作的能力。

在第四和第五项研究中，我们采用了一项摇板测试，以检验被试者被机械性连接在一起后单个被试者人和其他被试者之间的控制情况。在第四项研究中，我们假定视觉在个体运动协调中起重要作用，并因此重点调查视觉的重要作用。我们侧重于比较以下两种条件下预测性运动控制所占的比例。我们先要求两位被试者面对面站立（即可以看到对方），然后再背对背站立（即可以看不到对方）。我们还预计，在被试者完成此项重复性任务时要同时受空间和时间的限制，他们要么会利用生物力学的幅度-频率关系，要么采用一种认知方法以便控制幅度和频率。结果表明，在完成目标明确的任务时，生物力学是主要运动控制机制，且似乎不受其它知觉的影响。这些知觉是人体用来监测动作方式所产生的知觉结果的。

在第五项研究中，我们检验了关节协调模式的运动分析中的主关节假设（LJH）。在摇板测试中，被试者要按要求的角度和频率控制摇板。我们发现，对于每位被试者和各被试者来说，膝关节旋转是动作的基础，每位被试者的动作都要服从整体动作，以便在这个大空间重复性运动任务中实现对关节动作的小空间控制。

在最后一章中，我们将讨论本文报道的经验性研究结果。我们在实施研究中讨论了各种方法，即协调法、利用法、分配法和授权法。我们进一步探讨了某些悬而未决的问题，并为未来的研究提出了建议。本文的结论是，我们的研究对临床物理治疗学有重要价值。

总之，本文报道的研究证实，人体对过多的运动资源管理不仅受人体运动器官系统的解剖结构限制。一般地说，人体还能很聪明地利用运动系统的生物力学特性，为了实现运动目标而故意牺牲生物力学效能。另外，这些研究还证实，据信那些适用于个体运动控制的控制原理也适用于集体性动作。这些发现对物理治疗学有重要价值，这些已有详细论述。

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The author of this dissertation was born in Bussum, The Netherlands on September 17, 1949. He attended the Karachi Grammar School in Karachi, Pakistan from 1954 to 1965 and passed the final high school exam 'HBS-B' in 1971 at the Christelijk Lyceum in Veenendaal, The Netherlands. After completing the undergraduate course Bachelor of Physiotherapy in 1975 at the Hogeschool Utrecht (HU), The Netherlands, and Manuele Therapie, in 1978 at the School voor Manuele Therapie in Utrecht, The Netherlands, he successively worked as a physical therapist at the Surgical Intensive Care Unit at Universitair Medisch Centrum Utrecht (UMC), Asthma Center Heideheuvel, Hilversum and is currently engaged in primary health care at a private office in Doorn in The Netherlands. With the undergraduate thesis Non-linear aspects of joint coordination in blackboard writing, he completed the Master of Research course (MRes) 'Cognitive Neuroscience' headed by Prof. dr. G. P. van Galen and Prof. dr. B. Smits-Engelsman in 2001 at the Nijmegen Institute for Cognition and Information at the Radboud University, Nijmegen, The Netherlands. Since 2002 he is working on the PhD project Managing Redundancy at Multiple Levels of Motor Control under supervision by Prof. dr. R.G.J. Meulenbroek. This work resulted in the present doctoral dissertation.